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Errata

Page 135, line 12, for "*curea*" read "*aurea*."
Page 199, line 17, for "that to" read "to that."
Page 207, line 8, *D[esmatodon] neomexicanus* is a synonym of *D. plinthobius* (as stated on page 212) and not a species of *Tortula*.
Page 261, line 12, for "*Cladastris*" read "*Cladrastis*."
Page 305, line 2 from bottom, for "*ophoides*" read "*ophioides*."
Page 306, line 13, for "*racemosa*" read "*racemosus*."
Page 308, line 5, omit "*Aster laevis*."
Page 312, last line, for "*Graphalium*" read "*Gnaphalium*."
Page 318, line 15, for "*Tolmei*" read "*Tolmiei*."
Pages 335 and 336 are omitted.
Page 412, line 15 from bottom, for "*Phaksopsora*" read "*Phakopsora*."
Page 415, line 8 from bottom, for "*phaksopsoroides*" read "*phakopsoroides*."
Page 430, line 16, for "*memoralis*" read "*nemoralis*."
Page 431, line 8 from bottom, for "*humilus*" read "*humilis*."

No. 1

BULLETIN

OF THE

TORREY BOTANICAL CLUB

JANUARY, 1919

A study of some factors influencing the stimulative action of zinc sulphate on the growth of Aspergillus niger. II. A comparison of two strains of the fungus.

R. A. Steinberg

(WITH PLATE 1 AND FOUR TEXT FIGURES)

It will be apparent to those concerning themselves with the "stimulative" action of zinc sulphate on the growth of *Aspergillus niger* that marked discrepancies exist between the results reported by different investigators. These variations are most apparent in the yields (dry-weight per 50 c.c. of nutrient solution) obtained in the apparent absence of zinc, the maximum yield in the presence of the optimum concentration of zinc, and the minimum concentration of zinc necessary for the maximum yield.

Discussion of the variations apparent in the results reported will be confined to the following tabulation of the minimum concentration of zinc for maximum growth, as given by various authors:

Raulin (3).	10 61 mg Zn/L
Richards (4)	9.10 "
Ono (2)	8.41 "
Richter (5)	0.09 "
Javillier (1)	0.10 "

The differences are evidently too large to be laid to experimental errors.

The experiments taken up in this paper are concerned with observations made on two strains of *Aspergillus niger* over a

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period of somewhat more than six months. The evidence, though fragmentary, since many of the experiments had other purposes in view than that for which they are here utilized, is sufficiently full to be of value in indicating some of the factors responsible for the variations noted above.*

From cultures used in previous studies (labelled as originally from the "Internationalstelle für Pilz-Kulturen, Amsterdam"), two one-spore strains were isolated in the following manner:

A series of platings and transfers to agar (1 per cent. each of peptone, sucrose and agar) indicated that the cultures could be divided microscopically into two groups based on the relative abundance of yellow pigment in the hyphae. Two tubes were selected, one showing no yellow pigment and the other the maximum amount of yellow pigment; these served as the source material for the isolation of two one-spore strains.

Single drops of an agar dilution of the spores from these cultures were placed on sterile cover-glasses, and the cover-glasses inverted on Van Tieghem slides. These were placed in the thermostat at 30–31° C. After twenty-four hours the slides were examined (Leitz: 4 ocular, 8 objective) and only those retained in which but one conidium, and this germinated, could be seen. The bit of agar containing this single germinated spore was at once transferred from the coverglass to an agar slant. In another twenty-four hours these transfers had fruited and were again immediately transferred. Great care was taken in making this transfer not to touch the substratum but only the tops of the conidiophores. The cultures thus finally obtained are assumed to be one-spore cultures. They will be referred to as the W and Y strains, respectively. The presence of yellow pigment is more conspicuous in the latter.

The second transfer was considered advisable as a check on the possible presence of other conidia (ungerminated) overlooked in the microscopic examination made after the first twenty-four hours. Since a mycelium arising from a conidium does not fruit within twenty-four hours, any ungerminated conidium accident-

* In view of the results obtained by me, some of the experiments should be repeated and elaborated, but since this work has been indefinitely interrupted as a result of my being drafted into the army, I am publishing the data as they stand.

ally overlooked will not as yet have had time, even if it did develop, to have resulted in spore formation at the time of the second transfer.

The two strains thus isolated were kept on agar slants, of the composition given above, in the thermostat, at 30–31° C. Subcultures for the inoculation of the flasks (containing Pfeffer solution) were made on bread and were also kept in the thermostat at 30–31° C. The agar stock cultures were carried in duplicate, transfers being at irregular intervals. A duplicate stock culture once having been used either for the preparation of new stock cultures or of a bread culture was placed aside as unfit for further use. The practice was also made of preserving a single duplicate stock culture, unused, from each transfer.

The methods used in the experiments described below have already been given in detail in a previous publication (**6**). I may note briefly that all cultures were kept at 30–31° C., and that 150 c.c. pyrex Erlenmeyers were used. The Pfeffer nutrient solution was made up with water redistilled through glass, "Crystal Domino" cane-sugar, and Merck's "Reagent" NH_4NO_3 and $MgSO_4 \cdot 7H_2O$; the other compounds being the Baker "Analyzed." In one or two instances, in which Kahlbaum's "Zur Anal." $MgSO_4 \cdot 7H_2O$ was used, this fact is noted. Each culture in the pyrex flasks contained 50 c.c. of Pfeffer solution, the dry-weight or yield representing therefore the amount of tissue formed by the organism in such a culture. Inoculations at all times were from bread cultures. The period of growth of the cultures was in each case seven days.

The existence of quantitative differences between the two strains was quite clearly indicated in the very first experiment (EXP. I).*

	W	Y
No zinc	0.237 gram	0.546 gram
0.1 mg. Zn/L.	0.903 "	0.811 "

The yield of the W strain is less than half that of the Y strain in the apparent absence of zinc, whereas it is slightly greater than that of the Y strain in the presence of 0.1 mg. Zn/L.

* The detailed data for each experiment are given in the Appendix.

The next experiment (EXP. II) gave the following results.

	W	Y
No zinc.	0.317 gram	0.480 gram
0 01 mg. Zn/L	0.565 "	0.781 "

On the assumption that both strains could, even in the presence of the optimum concentration of zinc, produce not more than one gram of tissue, it is evident that a higher concentration of zinc would be necessary in the case of the W than of the Y strain in order to obtain the maximum yield.

The determination of the minimum concentrations of zinc required for the maximum production of tissue was made in quite a simple manner. An experiment was first performed in which zinc in widely different concentrations was used and the values desired thus located approximately as being between two of these concentrations. The next experiment was with concentrations between these limiting values and differing amongst themselves by amounts of 0.01 mg. Zn/L.

The first experiment which served for the approximate location of the zinc optima is here summarized (EXP. III).

	W	Y
0 0 mg Zn/L	0 217 gram	0 302 gram
0 001 "	0 418 "	0 620 "
0.05 "	0 725 "	0.847 "
0.1 "	0 877 "	0 805 "
1.0 "	0 915 "	0.798 "

These values are shown plotted in TEXT FIG. 1. The minimum concentration of zinc capable of bringing about maximum growth is, we note, approximately 0.1 mg. Zn/L for the W strain and about 0.05 mg. Zn/L for the Y strain. We observe, in addition, that the maximum yield of the former is slightly the greater.

The more accurate location of the values sought was attempted in a series of cultures differing in zinc content by 0.01 mg. Zn/L (EXP. IV).

W		Y	
0.0 mg. Zn/L	0.119 gram	0.0 mg. Zn/L	0.343 gram
0.07 "	0 805 "	0.02 "	0.844 "
0.08 "	0 900 "	0.03 "	0.803 "
0.09 "	0 940 "	0.04 "	0.806 "
0.10 "	0 825 "	0.05 "	0.847 "

Reference to figures given for EXPS. III and IV indicates that the yield concentration curves intersect in both cases at approximately 0.075 mg. Zn/L. With this concentration the yields with both strains under the conditions employed should be identical and equal to about 0.85 gram.

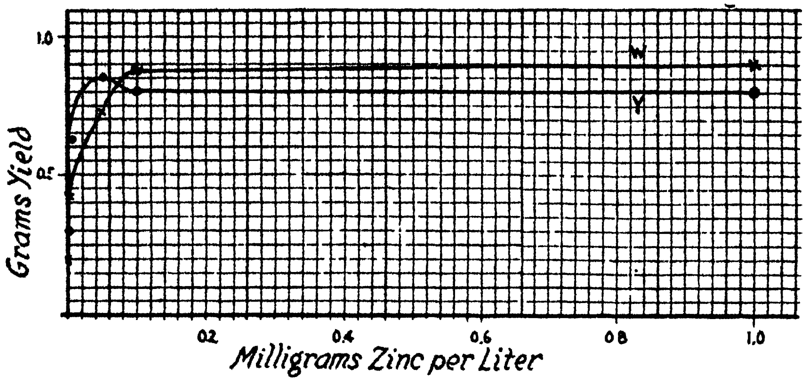

FIG. 1. For explanation see text.

The number of concentrations employed was evidently not sufficient to establish the precise location of the minimum zinc concentration producing the maximum yield, more particularly in the case of the Y strain; and, furthermore, a comparison of the yields obtained in this experiment with those obtained in the previously cited experiments shows that the organisms are not reacting uniformly to what are intended to be identical cultural conditions. This is brought out more conspicuously if we include in our consideration the results obtained several months later (EXPS. VIII and IX).

	W	Y
0.0 mg. Zn/L.	0.130 gram	0.205 gram
0.01 "	0.287 "	0.283 "
0.1 "	0.851 "	0.823 "
0.5 "	0.843 "	0.826 "
1.0 "	0.915 "	0.859 "
5.0 "	0.903 "	0.757 "
10.0 "	0.906 "	0.771 "
15.0 "	0.902 "	0.746 "
20.0 "	0.901 "	0.725 "
25.0 "	0.945 "	0.754 "

For these experiments also the yields have been plotted against zinc concentrations (TEXT FIG. 2).

On comparing the results obtained in this experiment with those of the preceding, we become aware of a curious phenomenon—the action of suboptimal zinc concentrations on the growth has become less effective. Whereas in EXP. II the addition of

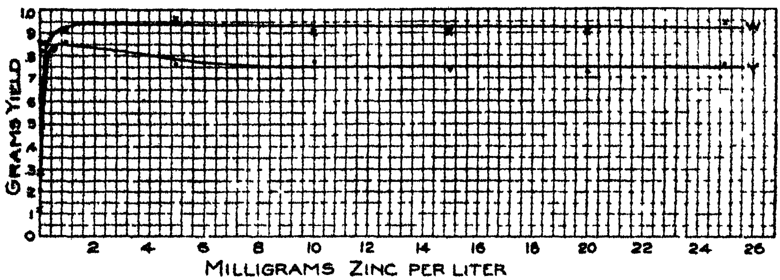

FIG 2. For explanation see text

0.01 mg. Zn/L to the cultures resulted in yields of 0.565 gram and 0.781 gram for the W and Y strains respectively, in EXPS. VIII and IX the corresponding yields were only 0.287 gram and 0.283 gram. Even with apparently zinc-free cultures the same change had taken place. In the earlier experiment just mentioned the yields in the apparent absence of zinc were 0 317 gram and 0.480 gram for the W and Y strains respectively; while now they are 0.136 gram and 0.205 gram. It would seem that for suboptimal zinc concentrations (or more precisely, concentrations below 0.1 mg. Zn/L), the initial differences between the W and Y strains with respect to the extent of growth have largely disappeared. The validity of this assumption will, however, again be discussed.

Finally, after culturing for thirty-one weeks on the peptone-sucrose agar, the tenth generation transfers of the two strains resulted in the following yields when inoculated into the flasks containing as usual each 50 c.c. of Pfeffer solution (EXP. XVIII).

	W	Y
0.0 mg. Zn/L	0 177 gram	0.222 gram
0.01 "	0.287 "	0.440 "
0.02 "	0.381 "	0.501 "
0.03 "	0 475 "	0.563 "
0.04 "	0.523 "	0.642 "
0.05 "	0 534 "	0.707 "

	W	Y
0.06 mg. Zn/L	0.688 gram	0.793 gram
0.07 "	0.697 "	0.753 "
0.08 "	0.758 "	0.734 "
0.09 "	0.761 "	0.770 "
0.10 "	0.800 "	0.799 "

The minimum concentrations of zinc necessary for the formation of maximum dry-weight is for the W strain probably greater, in this case, than 0.1 mg. Zn/L, and for the Y strain, approximately 0.06 mg. Zn/L. The yields in the absence of zinc are a trifle higher than in EXPS. VIII and IX. In the presence of 0.01 mg. Zn/L the yield of the W strain is identical in EXPS. VIII and XVIII; whereas the yield of the Y strain, though 0.283 gram in the preceding experiment, is in the present trial 0.440 gram.

Many of the cultures in EXP. XVIII were photographed and

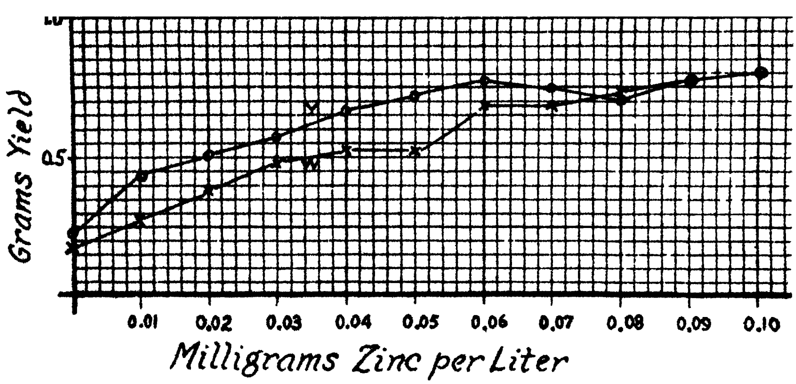

FIG. 3 For explanation see text.

are reproduced in PLATE I. In TEXT FIG. 3 the yields are shown plotted against the zinc concentrations.

To facilitate a survey of the changes in the yields obtained under supposedly identical conditions as these experiments progressed, the yields in "zinc-free" media for the entire period are summarized in the following table:

Both strains, it will be noted, showed a rapid decrease in respect to their capacity for growth in the Pfeffer solution. The two strains, nevertheless, are distinct in that the W always forms a smaller amount of tissue than the Y strain. The fact that a decrease in the capacity for growth has indeed taken place will

Weeks since isolation	Number of transfers	W	Y
1	Original	0.237 gram	0.546 gram
3	1	0.317 "	0.480 "
5	2	0.217 "	0.302 "
8	3	0.119 "	0.343 "
9	3	0.105 "	0.301 "
10	3	0.139 "	0.276 "
19	5	0.133 "	0.240 "
20	6	0.136 "	—
22	6	—	0.205 "
23	7	0.126 "	—
24	7	0.086 "	—
25	7	0.155 "	0.218 "
26	8	0.125 "	—
27	8	0.141 "	—
28	9	0.157 "	0.232 "
29	10	0.085 "	0.176 "
30	10	0.130 "	0.187 "
31	10	0.177 "	0.222 "

become more evident, in spite of the confusing experimental variations, on reference to the effect of constant amounts of zinc on the growth at different periods of time. Summarizing the yields obtained for the entire period with concentrations of 0.01 and 0.10 mg. Zn/L we find:

Weeks since isolation	Number of transfers	0.01 mg. Zn/l		0.10 mg. Zn/l	
		W	Y	W	Y
1	Original	—	—	0.903 g.	0.811 g.
3	1	0.565 g.	0.781 g.	—	—
5	2	—	—	0.877 "	0.805 "
8	3	—	—	0.825 "	—
20	6	0.287 "	—	0.851 "	—
22	6	—	0.283 "	—	0.823 "
30	10	0.198 "	0.268 "	—	—
31	10	0.287 "	0.440 "	0.800 "	0.799 "

The results obtained in "zinc-free" media and with media containing 0.01 mg. Zn/L are shown graphically in TEXT FIG. 4.

There is, it will be seen, a perceptible decrease in the yields obtained with both strains with time. While experimental variations due to at present unascertained conditions tend to obscure this phenomenon, a survey of the yields for identical zinc concentrations cannot but make evident that the capacity for growth of the organisms in the presence of small amounts of zinc has decreased. Not only the apparently zinc-free but also the zinc cultures exhibit the same result. Whereas strain

W when grown in the absence of zinc resulted initially in a yield of 0.237 gram, and the Y culture of 0.546 gram, the final yields were 0.177 gram and 0.222 gram. Similarly for the cultures grown in the presence of 0.01 mg. Zn/L, the initial yields were 0.565 gram and 0.781 gram and at the time of interruption of

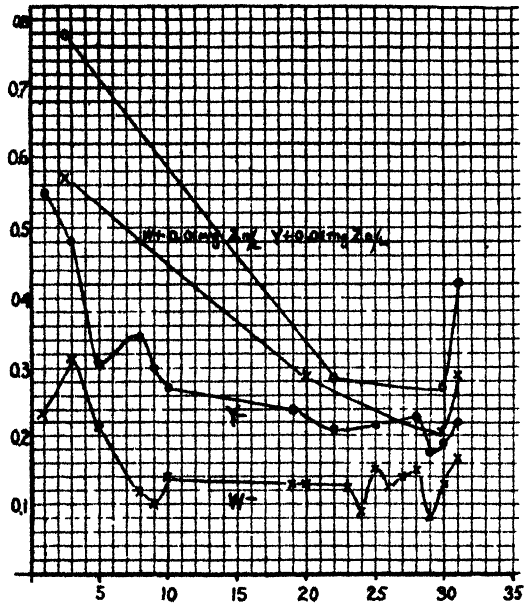

FIG. 4. For explanation see text.

the research but 0.287 gram and 0.440 gram for W and Y strains respectively. Other zinc concentrations display an analogous modification.

The progressive modification of the growth capacity hardly manifests itself, it can be observed, in the higher zinc concentrations. That is, by adding sufficient zinc the characteristic maximum yield of about 1 gram is obtained. A progressive change in the strains with respect to their sensitiveness to zinc would exhibit itself, it is rather likely, with higher zinc concentrations only after a considerable modification. The extent of the modification necessary would depend on the readiness with which the effects of slight fluctuation in zinc content at these concentrations could be perceived.

The same fact is presented to us from another angle if we con-

sider the minimum zinc concentration resulting in maximum yield; we find that the numerical value of this concentration increased as the experiments progressed, or, as previously stated, that in this respect also the sensitiveness of the organisms to the action of zinc has decreased.

Inspection of TEXT FIG. 4 suggests that to some extent at least the experimental deviations should be laid to an uncontrolled variation of the zinc concentration, or of other substances acting in the same direction. There is noticeable, for example, a decrease in the action of zinc (0.01 mg. Zn/L) as a rule when the simultaneous supposedly zinc-free cultures yield a weight below average. Similarly, the opposite-increased effectiveness of the action of zinc when the control cultures give a yield above average, is also evident on inspection of the curves for the twenty-eighth to thirty-first week inclusive.

In casting about for the causes underlying this gradual change in the strains, the assumption was made, that it was due to the non-addition of inorganic salts to the peptone-sucrose agar used for the stock cultures. This at least occurred to me as the simplest and most obvious explanation.

In order to test this assumption subcultures were made from the peptone-sucrose agar to other agar compositions containing various mineral salts. After three generations on the latter, they were used as usual for inoculating the liquid Pfeffer medium and the yields obtained compared with those obtained through the use of the standard peptone-sucrose spores. Thus transfers from the seventh generation cultures of the W and Y organisms cultured on the peptone-sucrose agar were made to a medium of the following composition:

	Water	1000.0 grams
	Sucrose	50.0 "
	Agar	10.0 "
Baker's "Analyzed"	NH_4NO_3	10.0 "
Baker's "Analyzed"	KH_2PO_4	5.0 "
Baker's "Analyzed"	$MgSO_4.7H_2O$	2.5 "
Baker's "Analyzed"	$Fe_2(SO_4)_3$	trace

Cultures on this medium are referred to as 7W and 7Y. In appearance they correspond quite closely to that of a zinc culture.

The membranes were thick and wrinkled, opaque, and white to light tan in color. Spores were present only in small amount. The third generation cultures on this composition (7W3 and 7Y3) were used for the inoculation of bread cultures and these in turn for the inoculation of the cultures on the Pfeffer nutrient solution according to the usual procedure. The average yields obtained were (EXP. XV):

Culture	Yield
W 9	0.157 gram
Y 9	0.232 "
7 W 3	0.147 "
7 Y 3	0.262 "

Apparently, no modification of the two strains had occurred by culturing on this agar composition for three generations, in so far as the yield obtained in the Pfeffer solution to which no zinc has been added is concerned.

An additional experiment gave similar results (EXP. XVII).

W 10		Y 10	
0.0 mg Zn/l	0.130 gram	0.0 mg Zn/l	0.187 gram
0.01 "	0.198 "	0.01 "	0.268 "
7 W 4		7 Y 4	
0.0 mg Zn/L	0.109 gram	0.0 mg Zn/L	0.175 gram
0.01 "	0.166	0.01 "	0.222

The results obtained by culturing in a similar manner on another medium led to apparently the same conclusion. The medium in this case consisted of 1 per cent. each of peptone, sucrose and agar. To this were added the salts (already tested by being used in the preparation of zinc-free Pfeffer solution) in the same amounts per liter as in the Pfeffer solution (p. 10). The cultures on this agar were similar in appearance to those on the zinc-free Pfeffer solution, agreeing in this respect with the peptone-sucrose agar cultures. A series of subcultures (8W and 8Y) were kept for three generations on the above medium (− 8W, − 8Y) and another series on the same medium to which 10 mg. Zn/L had been added (+ 8W, + 8Y). The results obtained on using this material for producing cultures on the liquid Pfeffer medium, to which no zinc was added (EXP. XVI), follow:

W 10	0.085 gram	Y 10	0.176 gram
− 8 W 3	0.135 "	− 8 Y 3	0.174 "
+ 8 W 3	0.114 "	+ 8 Y 3	0.179 "

In all the cases given, therefore, there is no evidence of an increase in the yield on the standard liquid Pefffer medium as a result of carrying the organism for three generations preceding inoculation of this medium on agar media containing various mineral salts—including zinc in some instances. This would indicate that the assumption made in attempting to account for the marked decrease in yields observed in the course of this investigation, namely, that the spores become impoverished in some essential ash constituent as a result of prolonged cultivation on peptone-sucrose agar, is improbable. The same conclusion is indicated by the result of EXP. XII, where about six months after the original separation of the two strains, cultures prepared by using spores of the original tubes (W1 and Y1) are compared with cultures prepared by using spores which had been on the peptone-sucrose agar for seven generations. The yields are practically identical.

The thought of course lies close at hand that changes occurred in the cultural conditions as the experiments progressed which are responsible for the changes in the yields obtained. Unusual precautions were taken, however, to maintain uniform conditions (see Steinberg, **6**). By consulting the data given in the Appendix it will be noted that the individual cultures of an experiment (as a rule five flasks of a kind were prepared) are very uniform. It is also to be noted that throughout the maximum yield of about 1 gram per 50 c.c. of medium was obtained, provided the proper amount of zinc was added, showing that the capacity for growth as such did not decrease. The fact that the decrease in yield is most conspicuous in cultures to which no zinc or to which only a small amount of zinc has been added suggests that the supposedly zinc-free media are actually not entirely free of this element. Zinc is an extremely troublesome element to eliminate completely from the chemicals and utensils employed. It is perhaps questionable whether thus far anyone has grown *Aspergillus niger* in the complete absence of zinc. In my own experiments it is conceivable that the pyrex flasks employed contain and give off to

the culture sufficient zinc (or other substances having a similar action) to influence the growth of the organism, even if zinc is not one of the ingredients entering into the formula for the manufacture of pyrex. On this assumption the decrease in the effect as the cultures are continued generation after generation could be laid to a leaching out of the element from the surface layers of the glassware. That the decrease would not be a steady one is to be expected from the well-known complexity of the solution processes taking place when glass is in contact with liquids. In addition it is to be assumed that there may be other uncontrolled sources of minute amounts of zinc, such as dust, etc. The differences in the behavior of the W and Y strains, as the experiments progressed, can be quite satisfactorily accounted for on the basis of the greater sensitiveness of the latter to the presence of zinc.

It is, therefore, quite probable that the differences existing in the literature between the results recorded by different investigators can, in part at least, be attributed to the use of strains having different zinc optima. While furthermore, possibly, the presence to varying degrees of unrecognized traces of zinc in the medium may have been an additional factor in producing these differences.

In conclusion, through the courtesy of Dr. Charles Thom, I am able to include a description of these strains based on his examination of cultures W5 and Y5.

"In both cultures the primary sterigmata measure 20 to 25 microns long by 3 to 6 microns in width. The secondary sterigmata are nearly uniform throughout the group and hence may be disregarded. The conidia are black when ripe, varying in both cultures considerably in diameter with an average of about 3½ to 4 microns, sometimes 5 microns. They are smooth at first, later more or less rough. The roughnesses in strain Y are somewhat less prominent than in strain W. These differences are differences in quantity only. The nature of the reaction is the same in each. These stalks of strain Y run 1,800 to 2,000 microns. In strain W they are about 700 microns long. They would therefore, fall respectively into section 2 and section 1 of *Aspergillus niger* as discussed by Thom and Currie, page 6" (7).

COLUMBIA UNIVERSITY

APPENDIX

Yields of the individual cultures, generally five of a kind. The number of weeks stated in connection with each experiment refers to the time elapsed since the original isolation of the two strains. For cultural conditions see page 3.

EXPERIMENT I

Kahlbaum's "Zur Anal." $MgSO_4.7H_2O$ used; 1 week

WO		YO	
No zinc	0.1 mg Zn/L	No zinc	0.1 mg Zn/L
* 0.910 gram	0.902 gram	0.509 gram	0.796 gram
0.219 "	0.868 "	0.510 "	0.804 "
0.230 "	0.894 "	0.531 "	0.809 "
0.289 "	0.910 "	0.607 "	0.820 "
0.211 "	0.942 "	0.575 "	0.827 "
0.237 "	0.903 "	0.546 "	0.811 "

EXPERIMENT II

Kahlbaum's "Zur Anal." $MgSO_4\ 7H_2O$ used; 3 weeks

W 1		Y 1	
No zinc	0.01 mg. Zn/L	No zinc	0.01 mg. Zn/L
0.302 gram	0.602 gram	0.516 gram	0.806 gram
0.265 "	0.578 "	0.535 "	0.830 "
0.339 "	0.562 "	0.546 "	0.843 "
0.330 "	0.528 "	0.409 "	0.694 "
0.335 "	0.554 "	0.393 "	0.732 "
0.317 "	0.565 "	0.480 "	0.781 "

EXPERIMENT III

5 weeks

W 2				
No zinc	0.001 mg. Zn/L	0.05 mg. Zn/L	0.1 mg Zn/L	1.0 mg. Zn/L
0.243 gram	0.335 gram	0.627 gram	0.861 gram	0.891 gram
0.246 "	0.392 "	0.750 "	0.862 "	0.923 "
0.175 "	0.397 "	0.703 "	0.843 "	0.947 "
0.217 "	0.507 "	0.760 "	0.890 "	0.904 "
0.205 "	0.461 "	0.785 "	0.929 "	0.912 "
0.217 "	0.418 "	0.725 "	0.877 "	0.915 "

* Accidental zinc culture. This phenomenon has been previously discussed (6).

Y 2

—mg. Zn/L	0.001 mg. Zn/L	0.05 mg. Zn/L	0.1 mg. Zn/L	1.0 mg. Zn/L
0.312 gram	0.622 gram	0.867 gram	0.797 gram	0.788 gram
0.347 "	0.686 "	0.823 "	0.822 "	0.774 "
0.265 "	0.458 "	0.893 "	0.825 "	0.799 "
0.263 "	0.618 "	0.825 "	0.790 "	0.804 "
0.323 "	0.718 "	0.825 "	0.789 "	0.822 "
0.302 "	0.620 "	0.847 "	0.805 "	0.798 "

EXPERIMENT IV

8 weeks

W 3

No zinc	0.07 mg. Zn/L	0.08 mg. Zn/L	0.09 mg. Zn/L	0.10 mg. Zn/L
0.143 gram	0.833 gram	0.947 gram	0.935 gram	0.806 gram
0.092 "	0.859 "	0.903 "	0.889 "	0.793 "
0.109 "	0.685 "	0.893 "	0.911 "	0.802 "
0.106 "	0.786 "	0.857 "	0.952 "	0.870 "
0.144 "	0.861 "	0.847 "	1.011 "	0.852 "
0.119 "	0.805 "	0.900 "	0.940 "	0.825 "

Y 3

No zinc	0.02 mg. Zn/L	0.03 mg. Zn/L	0.04 mg. Zn/L	0.05 mg. Zn/L
0.307 gram	0.818 gram	0.757 gram	0.786 gram	0.819 gram
0.377 "	0.836 "	0.831 "	0.848 "	0.857 "
0.296 "	0.855 "	0.786 "	0.828 "	0.875 "
0.369 "	0.850	0.846 "	0.757 "	0.812 "
0.366 "	0.856 "	0.794 "	0.812 "	0.872 "
0.343 "	0.844 "	0.803 "	0.806 "	0.847 "

EXPERIMENT V

9 weeks, no zinc

W 3	Y 3
0.127 gram	0.327 gram
* 0.908 "	0.362 "
0.078 "	0.341 "
0.081 "	0.206 "
0.133 "	0.268 "
0.105 "	0.301 "

EXPERIMENT VI

10 weeks

W 3		Y 3	
No zinc	0.09 mg. Zn/L	No zinc	0.09 mg. Zn/L
0.104 gram	0.822 gram	0.301 gram	0.822 gram
0.095 "	0.862 "	0.264 "	0.921 "
0.138 "	0.709 "	0.318 "	1.053 "
0.173 "	0.752 "	0.244 "	0.840 "
0.187 "	0.816 "	0.253 "	0.874 "
0.139 "	0.792 "	0.276 "	0.902

EXPERIMENT VII

19 weeks, no zinc

W 5	Y 5
0.133 gram	0.218 gram
0.124 "	0.252 "
0.146 "	0.263 "
0.140 "	0.250 "
0.121 "	0.218 "
0.133 "	0.240 "

EXPERIMENT VIII

20 weeks, W 6

No zinc	0.01 mg. Zn/L	0.1 mg Zn/L	0.5 mg. Zn/L	1.0 gm Zn/L
0.138 gram	0.298 gram	0.835 gram	0.817 gram	0.932 gram
0.137 "	0.295 "	0.828 "	0.817 "	0.803 "
0.174 "	0.289 "	0.885 "	0.824 "	0.972 "
0.104 "	0.290 "	0.835 "	0.840 "	0.910 "
0.125 "	0.263 "	0.871 "	0.916 "	0.958 "
0.136 "	0.287 "	0.851 "	0.843 "	0.915 "
5.0 mg. Zn/L	**10.0 mg Zn/L**	**15.0 mg. Zn/L**	**20.0 mg. Zn/L**	**25.0 mg Zn/L**
0.914 gram	0.880 gram	0.905 gram	0.947 gram	0.944 gram
0.932 "	0.869 "	0.871 "	0.860 "	0.952 "
0.979 "	0.903 "	0.894 "	0.901 "	0.915 "
0.967 "	0.941 "	0.923 "	0.914 "	0.943 "
1.024 "	0.939 "	0.917 "	0.883 "	0.973 "
0.963 "	0.906 "	0.902 "	0.901 "	0.945 "

EXPERIMENT IX

22 weeks, Y 6

No zinc	0.01 mg. Zn/L	0.1 mg. Zn/L	0.5 mg. Zn/L	1.0 mg. Zn/L
0.242 gram	0.270 gram	0.843 gram	0.808 gram	0.854 gram
0.180 "	0.342 "	0.836 "	0.832 "	0.865 "
0.203 "	0.274 "	0.828 "	0.825 "	0.843 "
0.190 "	0.256 "	0.798 "	0.835 "	0.864 "
0.208 "	0.274 "	0.811 "	0.829 "	0.871 "
0.205 "	0.283 "	0.823 "	0.826 "	0.859 "
5.0 mg. Zn/L	10.0 mg. Zn/L	15.0 mg. Zn/L	20.0 gm. Zn/L	25.0 mg. Zn/L
0.750 gram	0.791 gram	0.700 gram	0.706 gram	0.755 gram
0.736 "	0.759 "	0.756 "	0.723 "	0.725 "
0.739 "	0.774 "	0.760 "	0.747 "	0.739 "
0.740 "	0.772 "	0.734 "	0.703 "	0.776 "
0.821 "	0.759 "	0.779 "	0.746 "	0.773 "
		0.746 "	0.725	0.754

EXPERIMENTS X, XI AND XII

No zinc

X, 23 weeks	XI, 24 weeks	XII, 25 weeks			
W 7	W 7	W 7	W 1	Y 7	
0.211 gram	0.078 gram	0.170 gram	0.101 gram	0.270 gram	0.164 gram
0.907 "	0.082 "	0.183 "	0.119 "	0.273 "	0.262 "
0.196 "	0.091 "	0.148 "	0.066 "	0.200 "	0.245 "
0.112 "	0.087 "	0.123 "	0.098 "	0.180 "	0.198 "
0.112 "	0.090 "	0.153 "	0.107 "	0.160 "	0.212 "
0.126 "	0.086 "	0.155 "	0.098 "	0.218 "	0.216 "

EXPERIMENTS XIII AND XIV

W 8, no zinc

XIII, 26 weeks	XIV, 27 weeks
0.131 gram	0.136 gram
0.135 "	0.200 "
0.112 "	0.139 "
0.111 "	0.135 "
0.136 "	0.095 "
0.126 "	0.141 "

EXPERIMENT XV

28 weeks, no zinc

W 9	Y 9	7 W 3	7 Y 3
0 184 gram	0 247 gram	0 110 gram	0 255 gram
0 151 "	0 254 "	0 079 "	0 267 "
0 112 "	0 238 "	0 189 "	0 291 "
0 178 "	0 194 "	0 168 "	0 269 "
0 161 "	0 229 "	0 187 "	0 226
0 157 "	0 232 "	0 147 "	0 262 "

EXPERIMENT XVI

29 weeks, no zinc

W 10	−8 W 3	+8 W 3	Y 10	−Y 3	+8 Y 3
0 070 gram	0 145 gram	0 114 gram	0 167 gram	0 167 gram	0 191 gram
0 091 "	0 144 "	0 151 "	0 167	0 181	0 194
0 104	0 094 "	0 108 "	0 170	0 196	0 163
0 083	0 151 "	0 094 "	0 178	0 180 "	0 164
0 076 "	0 142 "	0 103 "	0 199	0 147 "	0 182 "
0 085 "	0 135 "	0 114 "	0 176	0 174	0 179

EXPERIMENT XVII

30 weeks

W 10		Y 10	
No zinc	0 01 mg Zn/L	No zinc	0 01 mg Zn/L
0 113 gram	0 195 gram	0 179 gram	0 199 gram
0 119 "	0 268 "	0 186 "	0 288
0 137 "	0 226 "	0 195 "	0 269
0 129	0 160 "	0 179 "	0 363 "
0 150	0 140 "	0 196 "	0 223 "
0 130 "	0 198 "	0 187 "	0 268 "

7 W 4		7 Y 4	
No zinc	0 01 mg Zn/L	No zinc	0 01 mg Zn/L
0 115 gram	0 212 gram	0 159 gram	0 197 gram
0 115 "	0 157 "	0 175 "	0 279 "
0 121 "	0 120 "	0 182 "	0 210 "
0 084 "	0 135 "	0 172 "	0 178 "
0 112 "	0 205 "	0 186 "	0 246 "
0 109 "	0 166 "	0 175 "	0 222 "

EXPERIMENT XVIII

3½ weeks

W 10

No zinc	0 01 mg Zn/L	0 02 mg Zn/L	0 03 mg Zn/L	0 04 mg Zn/L
0 203 gram	0 271 gram	0 386 gram	0 473 gram	0 525 gram
0 174 "	0 302 "	0 375 "	0 477 "	0 521 "
0 149 "				
0 196 "				
0 161 "				
0 177 "	0 287 "	0 381 "	0 475 "	0 523 "

0 05 mg Zn/L	0 06 mg Zn/L	0 07 mg Zn/L	0 08 mg Zn/L	0 09 mg Zn/L	0 10 mg Zn/L
0 466 gram	0 704 gram	0 698 gram	0 868 gram	0 722 gram	0 821 gram
0 602 "	0 671 "	0 695 "	0 647 "	0 799 "	0 779 "
0 534 "	0 688 "	0 697 "	0 758 "	0 761 "	0 800 "

Y 10

No zinc	0 01 mg Zn/L	0 02 mg Zn/L	0 03 mg Zn/L	0 04 mg Zn/L
0 186 gram	0 524 gram	0 517 gram	0 578 gram	0 650 gram
0 212 "	0 356 "	0 485 "	0 548 "	0 631
0 228 "				
0 252 "				
0 225 "				
0 222 "	0 440 "	0 501 "	0 563 "	0 642 "

0 05 mg Zn/L	0 06 mg Zn/L	0 07 mg Zn/L	0 08 mg Zn/L	0 09 mg Zn/L	0 10 mg Zn/L
0 674 gram	0 862 gram	0 765 gram	0 753 gram	0 765 gram	0 794 gram
0 739	0 724 "	0 741 "	0 715 "	0 785	0 804 "
0 707 "	0 793 "	0 753	0 734 "	0 770 "	0 799

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Explanation of plate 1

All photographs from EXP. XVIII

FIRST ROW. W strain. No zinc added to the cultures.

SECOND ROW. Y strain. No zinc added to the cultures.

THIRD ROW. W strain. Cultures contain from left to right 0.01, 0.02, 0.03, 0.04, 0.05 mg. Zn/L.

FOURTH ROW. W strain. Cultures contain from left to right 0.06, 0.07, 0.08, 0.09, 0.10 mg. Zn/L.

FIFTH ROW. Y strain. Cultures contain from left to right 0.01, 0.02, 0.03, 0.04, 0.05 mg. Zn/L.

SIXTH ROW. Y strain. Cultures contain from left to right 0.06, 0.07, 0.08, 0.09, 0.10 mg. Zn/L.

SEVENTH ROW. Cultures from left to right: W zinc-free, Y zinc-free, W 0.1 mg. Zn/L, Y 0.1 mg. Zn/L.

Notes on some western Lichens

R. S. Williams

Having occasion recently to write up the labels for a collection of lichens made in the Yukon region, in the years 1898 and 1899, and also for a small collection I made chiefly in the Blackfeet Indian Reservation of northern Montana, in the summer of 1897, I found a number of unnamed species and also various corrections which it seemed to me might be made.

Specimens from Yukon

The Yukon specimens were often in none too great quantity as they were picked up as occasion permitted without any previous preparation for that line of work. Duplicates of most of the Yukon collection I sent to the late T. A. Williams, of Washington, and to Miss Cummings, of Wellesley, and perhaps two thirds of these were determined by Mr. Williams, but no list published. Some years later another not very complete set was sent to Dr. R. Heber Howe and of these, determinations, partly made by Dr. Hasse, were published in the Bulletin of the Torrey Botanical Club (**38**: 287–293. 1911).

I now find in going over the original collection a number of species not seen by Dr. Howe and also some discrepancies owing, doubtless, partly to mixtures, lack of material or poor specimens. I shall first mention the Yukon plants not sent to Dr. Howe. They are the following well-known and widely distributed species:

Lecidea decipiens (Ehrh.) Ach.

Dawson, on rock, April, 1899 (*49*).

Lecidea granulosa (Ehrh.) Poetsch.

Hills above Lake Lindeman, May, 1898 (*50*).

Cladonia pyxidata (L.) Hoffm.

Lake Lindeman, May, 1898 (*4a*).

Rhizocarpon geographicum (L.) Lam. & DC.

Dawson, April, 1899 (*81*).

RHIZOCARPON PETRAEUM (Wulf.) Massal.
Dawson, very common (*101*).

PELTIGERA APHTHOSA (L.) Hoffm.
Lake Lindeman, May, 1898 (*34*).

NEPHROMOPSIS CILIARIS (Ach.) Hue.
Lake Lindeman, April, 1898 (*16*).

CETRARIA ISLANDICA CRISPA Ach.
Lake Lindeman, April, 1898 (*15a*).

PARMELIA PHYSODES (L.) Ach.
Dawson, common, October, 1898.

One species referred to in Howe's list, however, I do not find in my collection, namely, that under No. 11 in his enumeration, which is called *Biatora franciscana* Tuck. This was part of my collection number *56*; in what is left everything is evidently *Lecanora calcarea* (L.) Nyl., as determined by Dr. Hasse.

The remaining notes on Yukon specimens are taken up in order, according to Dr. Howe's numbers, and relate to changes, the numbers in parentheses being my collection numbers.

8. LECIDEA TESSELLATA Floerke. The specimen (*52*) was sent to Dr. Hasse, and referred to *Lecidea*, but was "too fragmentary for a satisfactory examination," in his opinion.

33. LECANORA LENTIGERA (Web.) Ach. On earth of river bluff just below Dawson, April, 1899 (*64*); evidently this, a fine and apparently rare species. Another specimen, however (*87*), questionably referred to *L. crassa*, under the impression that it was not distinct from *L. lentigera*, is certainly quite different from either. It is evidently *L. thamnoplaca* Tuck., not previously known north of Montana and but rarely collected. It was first obtained by Bolander in Nevada and next by Dr. Coulter in Yellowstone Park.

34. The specimens under this number, called *Lecanora thamnoplaca* Tuck., Dawson, April, 1898 (*51*), are all in my packet *Lecanora fruticulosa* (Dicks.) Ach.

35. The two collections here referred to *Lecanora pallida* have rather too large spores for that species. One (*63a*) has ellipsoid spores $\frac{40}{25}\,\mu$, which I should refer to *L. tartarea* (L.) Ach.; the other

(99), with spores $\frac{70}{35}$ μ, I should think *Ochrolechia pallescens* (L.) Massal. The spores of *L. pallida* (Schreb.) Schaer. are given as $\frac{9\text{–}20}{7\text{–}11}$ μ; otherwise *O. pallescens* is very similar to *L. pallida.*

36. Called *Lecanora subfusca* var. *argentea* Ach. This is certainly the same as No. 34, or *L. fruticulosa*, previously credited in North America only to California, I believe.

39. Called *Lecanora epibrya* Nyl. Dawson, July, 1898 *(30)*. My specimens apparently not distinct in any way from the preceding.

40. In my set none of the specimens under this number *(88)* are distinct from No. 34. *Lecanora castanea* (Hepp) Th. Fr., as given in Howe's list, does not seem to be represented.

53. All poor specimens under this number *(91)*, apparently charred by fire. They were doubtfully referred to *Ephebe pubescens* (L.) Fr. Collected at Dawson, July, 1898 *(91)*. I think the species is rather *Lecidea globifera* Ach., from which I believe *Biatora Russellii* Tuck. is not distinct.

56. This is typical *Solorina saccata* (L.) Ach., rather than the var. *spongiosa*, which it is called. Collected at Dawson, August, 1898 *(35)*. The other specimen under the name *S. saccata*, from Lake Lindeman, May, 1898 *(22)*, seems to be rather *Pannaria hypnorum* (Wahl.) Koerb. The spores are not more than $\frac{12}{8}$ μ and eight in the ascus. *Solorina saccata* has spores mostly four in the ascus and $\frac{36\text{–}55}{18\text{–}28}$ μ.

Three other species referred to in the list proved to be indeterminable in the duplicates sent out. I believe them to be as follows:

CLADONIA GRACILIS CHORDALIS Floerke.

Lake Lindeman, May, 1898 *(6)*.

BUELLIA COLLUDENS (Nyl.) Tuck.

Dawson, December, 1898 *(82)*, with no spores; Dawson June, 1899 *(82a)*, with spores two-celled, about $\frac{16}{7}$ μ, pale and eight in the ascus.

LECIDEA DECIPIENS (Ehrh.) Ach.

Dawson, on rock, April, 1899 (*49*). A widely distributed species.

SPECIMENS FROM MONTANA

ENDOCARPON TORTUOSUM Herre.

Near Big Badger Creek, Blackfeet Indian Reservation, September, 1897 (*92*). This species was described by Herre in 1911 from specimens collected near Reno, Nevada. I find no other record except these Montana specimens. The genus is peculiar in having oblong, muriform, brown spores, mostly two in the ascus; in this species measuring about $\frac{50}{18}\mu$.

ENDOCARPON PUSILLUM Hedw.

Heart Butte, September, 1897 (*100*). A much smaller species than the preceding, closely adnate to rocks and forming blackish discolorations. Spores similar to, and nearly as large as, the preceding, measuring about $\frac{45}{18}\mu$.

LECIDEA AMYLACEA Ach.

Henry Mountain, Blackfeet Indian Reservation, August, 1897 (*95*). We seem to have in the museum no specimen of this from North America. It is credited to Greenland and to Utah by Tuckerman.

LECIDEA ARMENIACA (DC.) Fr.

Blackfeet Indian Reservation, August, 1897 (*87*); fruiting. This species has been rarely collected in North America, and not before in fruit, I believe. In many respects, the plant is not so very unlike *Lecanora esculenta* of Arabia, which is supposed to be the manna of the ancient Jews. The taste is evidently quite similar.

ACAROSPORA RHAGADIOSA (Ach.) Fr.

On perpendicular walls of sandstone just below the Great Falls of the Missouri, February, 1889 (*90*); in fruit. This appears to be the only collection made of this species in North America. It seems a well-defined species, known previously only from Europe. The determination was by Nylander.

ACAROSPORA CERVINA (Wahl.) Koerb.

Two-medicine Lake, Blackfeet Indian Reservation, August, 1897 (*97*). This is a small western species, on rock, with apothecia more or less immersed and the ascus crowded with minute spores about $\frac{4}{2}\mu$. It has been mostly collected in California, under the name *Lecanora fuscata* (Schrad.) Th. Fr. This seems to be its most northern record.

ACAROSPORA CHLOROPHANA (Wahl.) Massal.

Henry Mountain, Blackfeet Indian Reservation, at 7000 ft., August, 1897. One of the most conspicuous of yellow, rock-loving species. The Golden Gate (or Gardiner) entrance to Yellowstone Park takes its name, I believe, from the quantity of this lichen covering the rock-walls near.

LECANORA ATRYNEA (Ach.) Nyl.

Near Two-medicine Lake, August, 1897 (*90*). The specimens more closely resemble some from the Pyrenees, determined by Nylander, than those from California collected by Herre. The California specimens are the only ones of North America in the museum, but it is mentioned in Miss Cummings's list of Alaska species as credited to that region by Dr. Almquest.

LECANORA THAMNOPLACA Tuck.

Columbia Falls, November, 1893, in fine fruit (*91*); also col-collected east of the Rocky Mountain Divide in Montana.

BLASTENIA FESTIVA (Fr.) Hasse.

Near Forty-mile Creek, Blackfeet Indian Reservation, August, 1897 (*106*). A small and inconspicuous rock-loving species. These Montana specimens appear to be the only ones collected outside of California in this country, but I believe are correctly referred here although the spores are not polar-bilocular as ordinarily occurs in this genus. Hasse states that the spores may be simply bilocular.

RINODINA CHRYSOMELAENA (Ach.) Tuck.

Forty-mile Creek, Blackfeet Indian Reservation, August, 1897 (*116*). This species has been but rarely collected and not before to the westward of the Mississippi, I believe.

NEW YORK BOTANICAL GARDEN

Apogamy in Camptosorus rhizophyllus*

Elizabeth Dorothy Wuist Brown

(WITH PLATE 2)

The life history of *Camptosorus rhizophyllus* (L.) Link, in both generations, has been studied in detail by Pickett.† An ecological study of the prothallia has also been published by the same author,‡ but no mention is made of observed cases of apogamy either in the field or in cultures. Neither has apogamy been recorded for this fern by any other investigator.

The case of apogamy described in this paper occurred in a culture of the fern which had been made, along with cultures of other ferns, to determine if apogamy could be induced by the modification of external conditions.

Material

Collections of the fertile fronds of *Camptosorus rhizophyllus* were made during the month of August from plants growing on the limestone cliffs of a glen in the vicinity of Ithaca, New York. They were allowed to dry by exposing the sealed envelopes, in which they had been placed in the field, to sunlight before an open window for about a week. For future use the envelopes were placed in a pasteboard box in the laboratory.

Cultures were made by sowing the spores thickly on 26 c.c. of Knop's full nutrient solution, to which had been added a drop of a 1 per cent. solution of ferric chloride, in small glass capsules. The formula of Knop's solution is as follows:

$MgSO_4$	0.25 gram
$Ca(NO_3)_2$	1.00 "
K_2HPO_4	0.25 "
KCl	0.12 "

* Contribution from the Osborn Botanical Laboratory.

† The development of the prothallium of *Camptosorus rhizophyllus*. Bot. Gaz. 57: 228–238. *pl. 12, 13* + *f. 1–8*. 1914.

‡ Some ecological adaptations of certain fern prothallia—*Camptosorus rhizophyllus* Link., *Asplenium platyneuron* Oakes. Amer. Jour. Bot. 1: 477–498. *pl. 49, 50* + *f. 1–10*. 1914.

After the spores had been sown the cultures were placed before an east window and the culture solutions were not renewed.

DEVELOPMENT OF THE PROTHALLIA

Germination began in about one week after the spores were sown and the growth and development of the prothallia were rapid at first, then slower as the amount of nutrient solution in the capsules decreased. The size and shape of the prothallia varied greatly. In the more crowded regions only a few developed into more or less heart-shaped prothallia, while the others in these regions were ribbon-shaped, irregular or branched. In the less crowded regions, especially near the margin of the cultures, more developed into heart-shaped prothallia. All the prothallia were smaller than when developed in cultures where the nutrient solution was renewed from time to time. Many of the prothallia showed the great irregularity of margin and the various types of marginal outgrowths described by Pickett. Antheridia in large numbers developed on the ribbon-shaped and branched prothallia, while the heart-shaped prothallia developed meristem which bore first antheridia and later archegonia. The latter evidently did not function, as no normal sporophytes were formed, although large quantities of antherozoids were present.

In about ten weeks after germination began, an apogamous sporophyte was found on one of the larger prothallia near the margin of the culture, in one of the less crowded regions. In a few weeks after the apogamous sporophyte developed, the nutrient solution in the capsules having been exhausted, new nutrient solution was added. The stimulating effect of this new solution could soon be noted by the appearance and growth of the prothallia and by the development of a few normal sporophytes. However, this stimulating influence seemed of short duration, as the culture soon began to decline. A number of the prothallia in the more crowded regions turned brown and appeared dead, while no more sporophytes were produced. When the solution was again exhausted new was added and again the stimulating influence could be noted, but it was not as noticeable as it had been before. The prothallia showed increased vigor, although no more sporophytes developed. Many of the prothallia which appeared dead gave rise to prolif-

erations which developed into prothallia bearing antheridia. Thus by adding new solution from time to time when the old became exhausted the culture has been kept living up to the present time. Some of the prothallia appear normal, having a meristem bearing both antheridia and archegonia, while others have given rise to proliferations which in turn bear antheridia.

DESCRIPTION OF THE APOGAMOUS GROWTH

The prothallium on which the apogamous outgrowth occurred was somewhat irregular in shape and only one cell in thickness (FIG. 1, P). No sinus was present and at the point where one usually occurs in larger and older prothallia a marginal structure, or lobe, had formed (FIG. 1, L).

The apogamous outgrowth began its development as a swelling in the region of the prothallium where the meristem begins to form. This swelling continued to grow, forming a cylindrical process several cells in thickness which became somewhat narrower as it developed. After growing for some time in this manner reversion to a narrow prothallus-like structure, only one cell in thickness with an irregular broadened apex (FIG. 1, AO), took place. At one point a branch, irregular in shape and itself showing a slight tendency to branch, developed (FIG. 1, B_1). On the opposite side of the prothallus-like structure, near the apex, another branch was formed. This branch-prothallium was somewhat elongated, one cell in thickness with a broad slightly heart-shaped apex (FIG. 1, B_2). Rhizoids developed from some of the marginal cells near the broadened apex (FIG. 1, R). On one side of the elongated part of this branch-prothallium, the marginal and adjacent cells were smaller and more numerous. From this region an archegonium, normal in appearance, developed (FIG. 1, A_1). The venter of the archegonium was not imbedded in the tissue of the prothallus but the whole archegonium extended beyond the margin of the prothallus (FIGS. 2, 3).

Two archegonia developed on the apogamous growth near its point of origin (FIG. 1, A_2) and just beyond this point a cluster of tracheids was formed in the tissue of the outgrowth (FIG. 1, T). As well as could be observed, owing to their imbedded position, these tracheids resembled those of a normal sporophyte.

DISCUSSION

Experimental data on induced apogamy would seem to indicate that bright light and insufficient moisture for fertilization were the controlling factors for the forms studied. In this particular case an insufficient food supply seems of greater importance than these two factors for the following reasons. Apogamy was never observed in other cultures of this fern under the same light conditions where the nutrient solution was renewed frequently. The prothallium upon which the apogamous outgrowth occurred, while developing near the margin of the culture, was crowded by other prothallia and shaded by them. Sufficient moisture for fertilization was available, as the prothallia developed upon a liquid medium. Later, when the nutrient solution was renewed, thereby supplying sufficient nourishment, normal sporophytes developed in the culture, although conditions of light and moisture remained unchanged. The fact that the part of the apogamous outgrowth which was last to develop showed a reversion from a more or less complex structure several cells in thickness bearing tracheids to a simple prothallus-like one only one cell in thickness and branched indicates a lowered vitality of the outgrowth. Goebel considers a reversion to a juvenile form as being the result of unfavorable conditions. The unfavorable condition in this instance was doubtless an insufficient food supply. However, the effect of this factor in inducing apogamy will be discussed at a greater length in a future paper on induced apogamy in *Phegopteris polypodioides* Fée.

Since only one case of apogamy was observed in the experimental cultures, it would seem that apogamy is of very rare occurrence in *Camptosorus* and not easily induced.

Explanation of plate 2

FIG. 1. Prothallium showing apogamous outgrowth, × 120: *P*, prothallium; *AO*, apogamous outgrowth; A_1, A_2, archegonia; *T*, tracheids; B_1, B_2, branches; *R*, rhizoids; *L*, lobe of prothallium

FIGS. 2, 3. Surface view and median optical section view of the archegonium borne on the margin of the branch of the apogamous outgrowth, × 275: *N*, neck; *C*, canal; *V*, venter; *E*, egg; *P*, prothallium.

INDEX TO AMERICAN BOTANICAL LITERATURE
1915–1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

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Xerophytic grasslands at different altitudes in Colorado

FRANCIS RAMALEY

(WITH TWO TEXT FIGURES)

The first comprehensive study of xerophytic grassland in Colorado was reported by Shantz (16) for the mesas at Colorado Springs. Later the same author (17, 18) published articles dealing with grasslands of the plains. Important work in the Pikes Peak region has been done by Clements (1, 2) and by Schneider (15). During the past few years the present writer (6, 7, 8, 9, 10, 11, 12) has published a number of papers dealing with dry grassland of the montane zone at Tolland, Colorado. In a contribution devoted chiefly to successions from marsh vegetation Robbins (14) also has given some points on dry grassland at Tolland. A rather brief but very clear and definite account by Vestal (20) of foothill grasslands, chiefly near Boulder, is included in a survey by him of the various associations of the foothill zone. An earlier paper by the same author (19) characterized the grasslands of the plains in the same locality. Fuller (3) has recently made a comparison of the dry grassland at Tolland with black soil prairie in Illinois.

Up to the present time there is no printed comparison of xerophytic grasslands at different altitudes in Colorado. Since these communities occur in large or small stretches all the way from the plains to alpine heights it is evident that very decided ecological and floristic differences must exist. These differences it is the aim of the present paper to report. Observations have been made on some of the areas for ten seasons. Certain localities have, however, been visited only a few times. During the prog-

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ress of the work a large collection has been accumulated which is kept as a special "dry grassland herbarium." Air temperature records have been kept for the growing season at Tolland (8,889 ft.) and these have been compared with reports from the government stations at Boulder (5,340 ft.) and at Corona (11,660 ft.). Soil temperatures have been carefully studied at Boulder and at Tolland, while occasional records have been made in the higher altitudes. The present work does not in any sense cover the whole

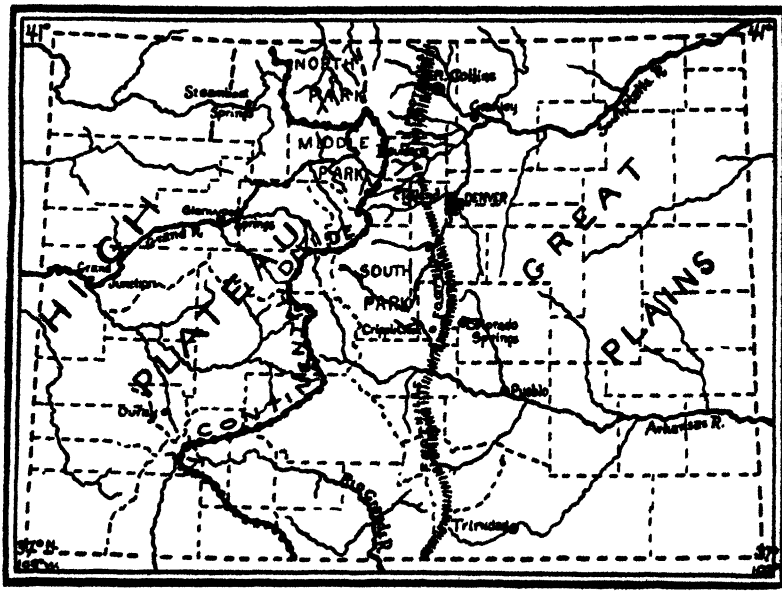

FIG. 1. Map of Colorado showing general geographic features. The Continental Divide extends in a zig-zag course north and south. The foothills at the mountain front are indicated by the series of horizontal lines. Boulder and Tolland are to the northwest of Denver.

of Colorado (FIG. 1) but merely the area tributary to the University at Boulder and the Mountain Laboratory at Tolland. Field work has been done chiefly in a rectangle about 40 miles east and west and 30 miles north and south with altitudes from 5,000 to 14,000 feet above sea level (FIG. 2).

In the following synopsis of xerophytic grasslands, descriptions are omitted because these are available in the writings of Shantz, Vestal, Pound and Clements (5), and the writer. Nichols's (4) exposition of ecological concepts has been followed in choosing names for the different communities. The nomenclature of species is that of Rydberg (13).

SYNOPSIS OF XEROPHYTIC GRASSLANDS IN NORTHERN COLORADO[1]

A. Associations of mixed character belonging to the plains region; not clearly dominated by grasses or sedges:

1. *Gutierrezia-Artemisia* Association.
2. Plains Ruderal Association.
3. *Chrysothamnus* Association.
4. *Artemisia filifolia* Consociation (of the Sand Hills Mixed Association).

B. Associations dominated by sedges; mountain communities not represented on the plains (Ramaley, **11**):

5. *Carex stenophylla* Grassland Association; foothills and montane.
6. *Carex Rossii* Grassland Association; montane and subalpine.
7. *Carex siccata* Grassland Association; montane and subalpine.
8. *Carex elynoides* Grassland Association; subalpine and alpine.

C. Associations of the Mixed Dry Grassland Type:

9. Inceptive Dry Grassland Association of the Foothill Zone (the Foothills Primitive Grassland of Vestal, **20**).
10. Derivative Dry Grassland Association of the Foothill Zone (the Foothills Mixed Grassland of Vestal, **20**).
11. Inceptive Dry Grassland Association of the Montane Zone.
12. Derivative Dry Grassland Association of the Montane Zone.

D. Associations dominated by one or a few species of grasses:

13. Short Grass Association; plains and mountain front; dominated by *Bouteloua* and *Bulbilis*.
14. Wheat Grass Association, mountain front chiefly; dominated by *Agropyron Smithii*.
15. *Andropogon* Bunch Grass Association; plains and mountain front.
16. Porcupine Grass Association; plains and foothills, occasionally montane; dominated by *Stipa*.
17. Sand Hills Mixed Association; plains; dominated by *Calamovilfa* and *Andropogon*.

[1] It is often difficult to decide just what communities should be included as "grassland." The writer omits lichen and mat associations, since they have almost no grasses or grass-like plants. Communities in which shrubs dominate are excluded; these are best known as "scrub." The Prairie Grass Association (of Vestal) is not included, as it is mesophytic.

18. *Festuca* Bunch Grass Association; montane; dominated by tall cespitose species of *Festuca.*
19. *Muhlenbergia-Danthonia* Consociation (of the Derivative Dry Grassland Association of the Montane Zone).

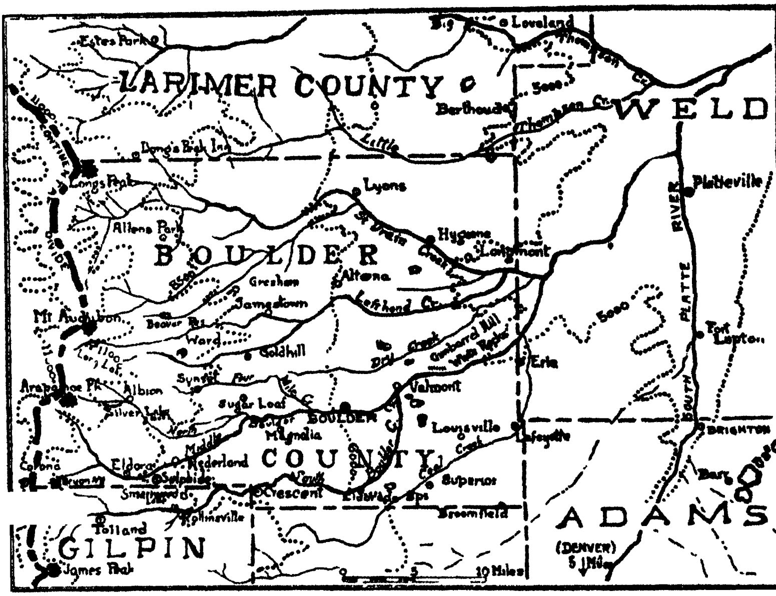

FIG. 2. Map of that part of Colorado readily studied botanically from the University of Colorado at Boulder and from the Mountain Laboratory at Tolland. Contour lines are shown for 5,000 ft., 6,000 ft., 8,500 ft., and 11,000 ft. The mountain front is at about 6,000 ft.

THE MIXED DRY GRASSLAND TYPE

The term "Mixed Dry Grassland," as used by the writer, includes all mountain grasslands of mixed character, growing generally in coarse-grained soil. In the preceding synopsis the communities numbered from 8 to 12 inclusive belong here and also Nos. 1 and 19. Early stages of the Short Grass Association, No. 13, are also of the Mixed Dry Grassland type. The Porcupine Grass Association, No. 16, when it occurs in montane situations may resemble ordinary montane dry grassland, and the *Festuca* Bunch Grass Association, No. 18, is, in places, not so very different. Indeed, any of the grassland associations of the mountains may belong to this general type.

While there is no difficulty in recognizing inceptive and derivative stages of the various dry grasslands the species concerned

are much the same. Thus, in the montane area, practically all the species present in the early stages persist throughout; the relative proportions change, however, and more species enter the association as the soil becomes finer grained and as humus accumulates.

Occurrence of these grasslands is wide spread. In the lower part of the foothill region typical vegetation is a coniferous savanna. In the interspaces between trees there is dry grassland. Many intervales, locally known as "parks," are almost entirely without trees. In both foothill and montane areas many stream terraces, alluvial fans, and south-facing hill slopes support dry grassland. In the subalpine zone conditions for forest development are more favorable, and grassland is likely to be confined to burned areas or to wind-swept south exposures.

ENVIRONMENTAL INFLUENCES

The stations where most of the collections were made, with their altitudes, are as follows:

Boulder, 5,340 ft.; mountain front, mesa area.
Crescent, 7,457 ft.; lower foothills.
Rollinsville, 8,367 ft.; upper foothills.
Sulphide, 8,508 ft.; upper foothills.
Smartweed Lake, 8,420 ft.; upper foothills.
Tolland, 8,889 ft.; montane.
Bryan Mountain, 11,000 ft.; subalpine.

Boulder, Crescent, Sulphide and Bryan Mountain are in Boulder County; Rollinsville, Smartweed Lake and Tolland are in Gilpin County (see FIG. 2). Many other stations through both of these counties have been visited.

The soil of all the dry grasslands is disintegrated rock, rather coarse grained, often with pebbles and boulders. It readily permits penetration of rain water but it dries quickly. As shown in a previous paper (10) the water content is low, averaging about 7 per cent, but the wilting coefficient is correspondingly low, about 5; figures being for 3 dm. depth. The soils warm up quickly through direct insolation and show a higher temperature than the air. Floristic differences in the dry grasslands do not depend on soil quality for this is much the same in all, but rather on air temperature (TABLE I), soil temperature (TABLE II), and pre-

TABLE I

MEAN TEMPERATURES IN DEGREES FAHRENHEIT. THOSE AT TOLLAND AND BRYAN MOUNTAIN ARE ESTIMATED, EXCEPT FOR JULY AND AUGUST AT TOLLAND

	Boulder 5,340 ft.	Tolland 8,889 ft.	Bryan Mt. 11,000 ft.
May	56	42	35
June	65	51	44
July	70	57	50
August	70	55	48
September	64	46	39

TABLE II

SOIL TEMPERATURES IN DEGREES FAHRENHEIT OF DRY GRASSLAND AT THREE TYPICAL ALTITUDES; NUMEROUS OBSERVATIONS AT 3 DM. DEPTH

	Boulder 5,340 ft.	Tolland 8,889 ft.	Bryan Mt. 11,000 ft.
May	55		
June	64	54	
July	72	64	58
August	70	62	56
September	64	58	52

Note.—Since readings of soil temperature were taken in the daytime they are somewhat above the true average. Data for Bryan Mountain are rather fragmentary and figures may have to be revised later. Probably the May soil temperature at Bryan Mountain is very low, close to freezing in the early part of the month.

cipitation. The mean annual rainfall at Boulder is 18 inches, at Tolland probably 28 inches, and at Bryan Mountain it can safely be estimated at 38 inches. April is the wettest month at all the stations. At the higher altitudes the greater rainfall and cooler temperature make the grasslands more mesophytic than those of plains and foothills.

SYSTEMATIC LIST OF SPECIES

A list of the species characteristic of xerophytic grasslands at various elevations is given below. Only spermatophytes and pteridophytes are recorded; lower plants, aside from parasitic fungi, are almost entirely unrepresented in dry grassland. It is of importance to note that in montane and subalpine situations, due to the more congenial climatic features mentioned above, a number of species, which in the lowlands are confined to moister soil, may be regular components of dry grassland. This distinction is brought out in the list: the letter *x* signifies that the species is present in dry grassland at that altitude; the letter *o* means that the species is found in moister places rather than in dry grassland at the altitude indicated. The letter *s* means that the species occurs at the altitude named, but only in special situations (where warm or protected) and is not a true component of dry grassland.

	Sub-alpine	Mon-tane	Upper foothill	Lower foothill	Moun-tain front
Selaginellaceae					
Selaginella densa	*x*	*x*	*x*	*x*	*x*
Poaceae					
Agropyron biflorum	–	*x*	*x*	–	–
" *molle*	–	–	*x*	*x*	*x*
" *pseudorepens*	–	*x*	*x*	*o*	*o*
" *Richardsoni*	–	*x*	*x*	*x*	*x*
" *Scribneri*	*x*	–	–	–	–
" *Smithii*	–	*s*	*x*	*x*	*x*
" *spicatum*	–	–	*x*	*x*	*x*
" *tenerum*	–	*x*	*x*	*o*	*o*
Andropogon Hallii	–	–	–	–	*x*
" *provincialis*	–	–	–	–	*x*
Aristida longiseta	–	–	–	*x*	*x*
Avena Hookeri	–	*x*	–	–	–
" *Mortoniana*	*x*	–	–	–	–
Blepharoneuron tricholepis	–	*x*	*x*	–	–
Bouteloua curtipendula	–	–	–	*x*	*x*
" *gracilis*	–	–	*x*	*x*	*x*
" *hirsuta*	–	–	*x*	*x*	*x*
Bromus brizaeformis (introduced)	–	–	–	–	*x*
" *Pumpellianus*	–	*x*	*x*	–	–
Bulbilis dactyloides	–	–		–	*x*
Calamagrostis purpurascens	*x*	*x*	*x*	–	–
Danthonia intermedia	*x*	*x*	–	–	–
" *Parryi*	–	*x*	*x*	–	–
Elymus triticoides		–	–	*x*	*x*
Eriocoma hymenoides	–			*x*	*x*
Festuca brachyphylla	*x*	–	–	–	–
" *ingrata*	–	*x*	*x*	–	–
" *minutiflora*	*x*	*x*	–	–	–
" *octoflora*	–	–	–		*x*
" *rubra*	–	*x*	*x*		–
" *saximontana*	*x*	*x*	*x*	–	*x*
Hesperochloa Kingii	–	*s*	*x*	*x*	*x*
Hordeum jubatum	–	*x*	*x*	*o*	*o*
" *nodosum*	–	–	*x*	*x*	*x*
Koeleria gracilis		*x*	*x*	*x*	*x*
Muhlenbergia gracilis	–	*x*	*x*	*x*	*x*
" *gracillima*	–	–		*x*	*x*
" *Richardsonis*	–	*x*	*x*	*x*	*x*
" *subalpina*	–	*x*	*x*		–
Pleuraphis mutica	–	–	–	–	*x*
Poa arctica	*x*	*x*	–	–	–
" *compressa*	–	*x*	*x*	*x*	*x*
" *confusa*	*x*	–	–	–	–
" *crocata*	*x*	*x*	*x*	*x*	–
" *epilis*	*x*	*x*	–	–	–
" *Fendleriana*	–	–	–	*x*	*x*
" *interior*	–	*x*	*x*	*o*	*o*
" *longipedunculata*	–	*x*	*x*	*x*	*x*
" *paddensis*	*x*	*x*	–	–	–
" *Pattersoni*	*x*	*x*	–	–	–
" *pratensis*	–	*x*	*x*	*o*	*o*
" *rupicola*	*x*	*x*	–	–	–
" *subaristata*	*x*	*x*	*x*	*x*	*x*

	Sub-alpine	Mon-tane	Upper foothill	Lower foothill	Moun-tain front
Poaceae—*continued*					
Schedonnardus paniculatus	–	–	–	*x*	*x*
Schizachyrium scoparium	–	–	–	*x*	*x*
Sitanion elymoides	–	*x*	*x*	*x*	*x*
Sorghastrum nutans	–	–	–	–	*x*
Sporobolus asperifolius	–	–	–	–	*x*
" *heterolepis*	–	–	–	–	*x*
Stipa comata	–	*x*	*x*	*x*	*x*
" *minor*	–	*x*	*x*	–	–
" *Nelsonii*	–	*x*	*x*	*x*	–
" *Tweedyi*	–	–	*x*	*x*	*x*
" *viridula*	–	*x*	*x*	*x*	*x*
Trisetum majus	–	*x*	*x*	–	–
" *subspicatum*	*x*	*o*	–	–	–
Cyperaceae					
Carex elynoides	*x*	*x*	–	–	–
" *heliophila*	–	*x*	*x*	*x*	*x*
" *obtusata*	–	*x*	*x*	–	–
" *oreocharis*	–	*x*	*x*	*x*	*o*
" *Rossii*	*x*	*x*	–	–	–
" *siccata*	*x*	*x*	–	–	–
" *stenophylla*	–	*x*	*x*	*x*	*x*
" *xerantica*	–	*x*	*x*	*x*	*x*
Melanthaceae					
Anticlea elegans	*x*	*o*	*o*	–	–
Toxicoscordion gramineum	–	–	–	*x*	*x*
Juncaceae					
Juncoides spicatum	*x*	–	–	–	–
Juncus ater	–	*x*	*x*	*o*	*o*
" *interior*	–	–	–	*x*	*x*
Alliaceae					
Allium recurvatum	–	*x*	*x*	*x*	*x*
" *textile*	–	–	–	*x*	*x*
Liliaceae					
Leucocrinum montanum	–	–	–	*x*	*x*
Lloydia serotina	*x*	–	–	–	–
Dracaenaceae					
Yucca glauca	–	–	–	*x*	*x*
Calochortaceae					
Calochortus Gunnisonii	–	*x*	*x*	*o*	*o*
Polygonaceae					
Eriogonum alatum	–	–	*x*	*x*	*x*
" *effusum*	–	–	–	–	*x*
" *flavum*	–	–	*x*	*x*	*x*
" *Jamesii*	–	–	–	*x*	*x*
" *umbellatum*	–	*x*	*x*	*x*	*x*
Polygonum Engelmannii	–	*x*	*x*	*x*	*x*
" *sawatchense*	–	–	*x*	*x*	*x*
Chenopodiaceae					
Chenopodium desiccatum	*s*	–	*x*	*x*	*x*
Nyctaginaceae					
Allionia linearis	–	–	–	*x*	*x*
" *pilosa*	–	–	–	*x*	*x*

	Sub alpine	Montane	Upper foothill	Lower foothill	Mountain front
Corrigiolaceae					
Paronychia Jamesii		—		x	x
Alsinaceae					
Alsinopsis obtusiloba	x	x	—	—	
Arenaria Fendleri	x	x	x	x	
Cerastium Beeringianum	x				
" *brachypodum*	—	—	—	x	x
" *campestre*	—		x	x	x
" *strictum*		x	x		
Caryophyllaceae					
Silene acaulis	x				—
" *Hallii*	—	x	x		
Ranunculaceae					
Delphinium Penardii					x
" *virescens*	—		—		x
Pulsatilla ludoviciana	x	o	o	o	o
Papaveraceae					
Argemone intermedia	—		—	x	x
Brassicaceae					
Cheirinia aspera	—	—	—	x	x
" *asperrima*	—			x	x
" *oblanceolata*	x	x	x	x	
" *Wheeleri*		x	x	x	
Draba coloradensis				x	x
Lepidium densiflorum			x	x	x
Lesquerella montana			x	x	x
Physaria floribunda		—	x	x	x
Thlaspi coloradense	x	x	x	x	x
" *purpurascens*	x	x	—		
Crassulaceae					
Sedum stenopetalum	x	x	x	x	x
Saxifragaceae					
Micranthes rhomboidea	x	x	x	o	o
Rosaceae					
Drymocallis glandulosa	—	x	x	x	x
Potentilla concinna		x	x		
" *effusa*		x	x	x	x
" *Hippiana*		x	x	x	x
" *strigosa*		x	x	x	x
Fabaceae					
Aragallus albiflorus	—	—	x	x	x
" *deflexus*		x	x		
" *Lambertii*		x	x	x	x
" *Richardsonii*	—	x	x	—	
Astragalus sulphurescens	—	x	x	—	
Geoprumnon succulentum	—			x	x
Homalobus flexuosus		x	x	x	x
Orophaca tridactylica				x	x
Petalostemon oligophyllus	—				x
" *purpureus*	—				x
Psoralea argophylla	—			—	x
Psoralea tenuiflora		—		x	x

	Sub-alpine	Mon-tane	Upper foothill	Lower foothill	Moun-tain front
Fabaceae—*continued*					
Tium Drummondii	–	–	–	*x*	*x*
Xylophacos Parryi	–	*x*	*x*	–	–
" *Purshii*	–	–	–	*x*	*x*
" *Shortianus*	–	–	*x*	*x*	*x*
Geraniaceae					
Geranium Fremontii	–	*s*	*x*	*x*	*x*
" *Parryi*	–	–	*x*	*x*	*x*
Linaceae					
Linum Lewisii	–	*x*	*x*	*x*	*x*
Euphorbiaceae					
Tithymalus robustus	–	*s*	*x*	*x*	*x*
Malvaceae					
Sphaeralcea coccinea	–	–	–	*x*	*x*
Violaceae					
Viola Nuttallii	–	–	–	*x*	*x*
Cactaceae					
Coryphantha missouriensis	–	–	*x*	*x*	*x*
" *radiosa*	–	–	*x*	*x*	*x*
Opuntia fragilis	–	–	–	*x*	*x*
" *polyacantha*	–	–	–	*x*	*x*
Onagraceae					
Gaura coccinea	–	–		*x*	*x*
" *glabra*		–	–	*x*	*x*
Meriolix serrulata	–	–	–	*x*	*x*
Ammiaceae					
Aletes acaulis	–	–	–	*x*	*x*
Cogswellia macrocarpa	–	–	–	*x*	*x*
" *orientalis*	–	–	–	*x*	*x*
Harbouria trachypleura	–	–	*x*	*x*	*x*
Musineon divaricatum	–	–	–	*x*	*x*
" *pedunculatum*	–	–	–	*x*	–
Oreoxis alpina	*x*	–	–	–	–
Pseudocymopterus tenuifolius	–	*x*	*x*	–	–
Primulaceae					
Androsace diffusa	–	–	*x*	*x*	–
" *occidentalis*	–	–	–	*x*	*x*
" *subumbellata*	*x*	*x*	–	–	–
Gentianaceae					
Dasystephana Bigelovii	–	–	*x*	*x*	–
Tessaranthium stenopetalum	–	*x*	*x*	*x*	*o*
Asclepiadaceae					
Acerates angustifolia	–	–	–	–	*x*
" *viridiflora*	–	–	–	–	*x*
Asclepias pumila	–	–	–	–	*x*
Polemoniaceae					
Collomia linearis	–	–	*x*	*x*	*o*
Gilia scariosa	–	–	*x*	*x*	–
" *spicata*	–	–	*x*	*x*	*x*
Phlox multiflora	–	–	–	*x*	–
Polemonium confertum	*x*	–	–	–	–

	Sub alpine	Montane	Upper foothill	Lower foothill	Mountain front
Hydrophyllaceae					
Phacelia heterophylla		x	x	x	x
" *sericea*	x	o	—		—
Boraginaceae					
Mertensia Bakeri	—	x			
" *cana*	x			—	—
" *lanceolata*			x	x	x
" *lateriflora*		x	x		—
" *lineariloba*			x		
" *Parryi*	x				—
Oreocarya virgata		x	x	x	x
Onosmodium occidentale		—			x
Verbenaceae					
Verbena bracteosa					x
Lamiaceae					
Hedeoma hispida ..				—	x
Monarda pectinata ..					x
Scrophulariaceae					
Castilleja occidentalis	x				—
sessiliflora					x
Orthocarpus luteus		x	x		
Pentstemon gracilis				x	x
Plantaginaceae					
Plantago Purshii			x	x	x
Rubiaceae					
Galium boreale		x	x	o	o
Santalaceae					
Comandra pallida		x	x	x	x
Campanulaceae					
Campanula petiolata	x	x	x	o	o
Ambrosiaceae					
Ambrosia psilostachya			x	x	x
Carduaceae					
Achillea lanulosa	x	x	x	o	o
Antennaria anaphaloides	x	x	x		—
aprica	x	x	x	x	x
arida		x	x	x	
campestris					x
microphylla		x	x	x	x
Artemisia aromatica		x	x	x	x
Brittonii	—		x	x	x
Forwoodii		x	x	x	x
frigida		x	x	x	x
" *gnaphaloides*		x	x	x	x
" *Pattersoni*	x				
Aster crassulus					x
" *Porteri*			x	x	x
*Chrysopsis asprella**	x	x	x	x	x
" *foliosa*		x	x	x	x

* The species of *Chrysopsis* are difficult of separation and it is possible that what the writer has separated as *C. asprella* and *C. hispida* should be combined, also that those listed as *C. foliosa* and *C. villosa* are a single species

	Sub-alpine	Mon-tane	Upper foothill	Lower foothill	Moun-tain front
Carduaceae—*continued*					
Chrysopsis fulcrata	–	–	*x*	*x*	*x*
" *hispida*	–	–	–	*x*	*x*
" *villosa*	–	*x*	*x*	*x*	*x*
Cirsium undulatum	–	–	–	*x*	*x*
Coreopsis tinctoria	–	–	–	–	*x*
Erigeron canus	–	–	–	–	*x*
" *compositus*	*x*	*x*	*x*	–	–
" *divergens*	–	*s*	*x*	*x*	*x*
" *flagellaris*	–	*x*	*x*	*x*	*x*
Gaillardia aristata	–	*x*	*x*	*o*	*o*
Grindelia erecta	–	*x*	*x*	–	–
" *perennis*	–	–	*x*	–	–
" *squarrosa*	–	–	*x*	*x*	*x*
" *subalpina*	–	*x*	*x*	–	–
Gutierrezia Sarothrae	–	–	–	*s*	*x*
Helianthus petiolaris	–	–	–	*x*	*x*
Hymenopappus filifolius	–	–	–	*x*	*x*
Kuhnia glutinosa	–	–	–	–	*x*
Laciniaria punctata	–	–	–	*x*	*x*
Machaeranthera aspera	–	–	–	*x*	*x*
" *varians*	–	*x*	*x*	–	–
" *viscosa*	–	*x*	*x*	–	–
Ratibida columnifera	–	–	–	–	*x*
Senecio oblanceolatus	–	–	–	*x*	*x*
" *perplexus*	–	*x*	*x*	*o*	*o*
" *plattensis*	–	–	–	–	*x*
" *spartioides*	–	–	–	*x*	*x*
" *werneriaefolius*	*x*	*o*	*o*	–	
Sideranthus spinulosus	–	–	–	–	*x*
Solidago concinna	–	*x*	*x*	–	–
" *decumbens*	*x*	*x*	–	–	–
" *missouriensis*	–	–	*x*	*x*	*x*
" *nana*	–	–	–	*x*	*x*
" *oreophila*	–	*x*	*o*	–	–
Tetraneuris acaulis	–	–	–	*x*	*x*
" *lanigera*	*x*	–	–	–	–
Tonestus pygmaeus	*x*	–	–	–	–
Townsendia exscapa	–	–	–	*x*	*x*
" *grandiflora*	–	–	*x*	*x*	*x*
Cichoriaceae					
Agoseris glauca	–	*x*	*x*	*x*	*x*
" *purpurea*	–	–	*x*	*x*	*o*
Lygodesmia juncea	–	–	–	–	*x*

FLORISTIC DIFFERENCES OF DRY GRASSLANDS AT DIFFERENT ALTITUDES

The foregoing systematic list gives in brief form the chief facts of altitudinal distribution of the various species in the dry grasslands. At the mountain front, i. e., on the mesas and mesa terraces, there are 160 species. In the lower foothills this number

is reduced to 139, in the higher foothills to 130, in the montane area to 107, and in the subalpine area to 50. It will be seen that there is a reduction in species roughly corresponding to increase of altitude. But the change from the montane dry grassland (at Tolland) to the subalpine dry grassland (at Bryan Mountain) is very abrupt.

It is sometimes difficult to decide whether a given species is to be included as properly belonging to a certain grassland. The attempt has been to exclude stragglers and accidental members, in other words to keep the lists reasonably small.

While the systematic list tells what particular species are found at the various stations it gives little idea of the true appearance of each grassland area. At the mountain front, as already noted, there is a great variety of plants. The average height of the vegetation is taller than elsewhere; many of the grasses and other plants are 3–6 dm. tall, and some are taller. Certain species are conspicuous which either do not occur at all higher up or else are infrequent, as, for example, *Agropyron spicatum*, the Andropogons, *Bromus brizaeformis; Yucca glauca*, the Delphiniums, the Petalostemons, *Tium Drummondii*, the various Cactaceae, the Gauras, *Helianthus petiolaris*, *Laciniaria punctata*, and *Ratibida columnifera*.

At Tolland the number of species is still large but a certain few are especially abundant and dominate wide areas, as, for example, the following: *Mertensia Bakeri*, which flowers in May; *Aragallus Lambertii*, which flowers in early July; *Sedum stenopetalum*, in mid-July; *Campanula petiolata* and *Orthocarpus luteus*, in August. The average height of vegetation in midsummer is 2–3 dm. Grasses and sedges are abundant, especially where the soil has considerable humus. Here the dry grassland becomes what the writer calls the *Muhlenbergia-Danthonia* Consociation (of the Derivative Dry Grassland Association of the Montane Zone.)

The dry grassland at Bryan Mountain (*Carex elynoides* Association) has a rather striking appearance because of the tufted masses of the dominant plant. This is, however, of low growth and the association does not look at all like the bunch grass association of the plains. Conditions are somewhat mesophytic on account of low temperature and frequent showers, so that many

of the plants recorded as belonging to the dry grassland would also be included in a list of mesophytes. One-third of the species are grasses.

The systematic list includes a total of 256 species in 131 genera and 35 families. The families best represented with the number of genera and species in each are shown below:

Poaceae	25	66	Rosaceae	2	6
Cyperaceae	1	8	Fabaceae	9	16
Polygonaceae	2	7	Ammiaceae	6	8
Alsinaceae	3	6	Boraginaceae	3	8
Brassicaceae	6	10	Carduaceae	23	55

Only 5 species range the whole distance from mountain front to subalpine zone. Of the 50 species at Bryan Mountain 29 extend down to Tolland and only 5 to the mountain front at Boulder. Of the 160 species at Boulder 40 range up to Tolland and 5 continue to Bryan Mountain. Floristically, then, the dry grasslands at Boulder and at Bryan Mountain are almost totally different, while a very considerable similarity exists between those of Boulder and Tolland and of Tolland and Bryan Mountain.

SUMMARY

The foregoing paper is based upon a study of grasslands in northern Colorado from the plains to the subalpine zone. A list is presented of all recognized xerophytic grassland communities in northern Colorado. From this list the author selects for comparison those of the "mixed dry grassland type." Environmental influences, the soil, temperature and rainfall are considered; the very low air and soil temperatures of the subalpine region being noted. To show floristic changes with altitude a systematic list of dry grassland plants is printed and the altitudinal distribution of each species indicated. At the mountain front there are 160 species in the dry grassland, while the numbers at other stations are as follows: lower foothills 139, upper foothills 130, montane area 107, subalpine area 50. Of the last named nearly one-half are strictly high-altitude forms which do not extend down even to the montane zone. It is pointed out that a number of species belonging to moister situations in the lowlands are able to enter dry grasslands of higher altitudes because of lower temperature

and greater rainfall there. A brief statement is made of differences in the grasslands not at once apparent from the systematic list. Floristically the dry grasslands of the mountain front and of the subalpine zone are almost totally different, but considerable similarily exists between those of the mountain front and of the montane zone.

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Additions to the flora of Colorado

Geo. E. Osterhout

1. **Nuttallia hastata** sp. nov.

Biennial, 4-8 dm. high, scabrous throughout as other like species of the genus, branched from the upper half, or even lower, the branches strict and somewhat fastigiate, flowers from the ends of the stem and branches, somewhat cymous; lower leaves narrowly linear, 5–10 cm. long, sinuate and bluntly dentate, tapering to a petiole, upper leaves linear-hastate, attached by a broad base, deeply dentate with sharp teeth, acuminate; flowers white, petals eight to ten, about 2 cm. long, the alternate ones smaller and more pointed, but seldom anther-bearing, capsules variable in length, the longer ones about 3 cm. long, four- to five-angled, usually a pair of bracts at the base; seeds under a good lens thickly and evenly papillose, wing-margined.

I have collected *Nuttallia hastata* at different times in several localities in Colorado, North Park, Middle Park, and Glenwood Springs, and not far from Jelm Post Office, Wyoming, by the roadside, on the east side of the Laramie River. The specimens which I have selected for the type were collected near Walden, North Park, Colorado, August 5, 1918, No. 5706. It does not closely resemble *N. nuda* (Pursh) Greene or *N. stricta* (Osterhout) Greene, but is what I suppose has been classified as *N. Rusbyi* (Wooton) Rydb. among the Colorado species. The flowers, however, are white, not yellow; and the capsule is angled, not cylindrical. Professor Wooton, in the original description of *N. Rusbyi*, observed, "stigma three-parted," but this is characteristic of a number of species, perhaps of the genus.

There is a peculiarity in the species of *Nuttallia* in that the flowers do not hold their color in the dried state. In the "Flora of the Rocky Mountains and adjacent plains," Dr. Rydberg says of the white flowered species, "petals straw-colored," and this is their appaerance by the time they usually reach the herbarium, but at the time of opening they are white, as far as I am acquainted with them, pure white.

2. **Phacelia formosula** sp. nov.

Biennial, 1.5–2 dm. high, stem single and upright, the flowering branches from near the top, or more commonly branched from near the base, the assurgent branches almost equaling the main stem, densely pubescent and somewhat hispid, becoming more glandular and hispid above; leaves lanceolate, or some of them oblanceolate, in outline. 5–7 cm. long pinnate with leaflets 5–10 mm. long, 3–5 mm. wide, entire or toothed, a terminal portion lobed or pinnatifid, not much enlarged, hispid with rather short hairs, the upper more glandular; inflorescence of several branches of two-ranked scorpoid racemes becoming 3 5 cm. long, corolla blue, its lobes rounded and entire, the filaments and style long-exserted; mature capsule the length of the calyx lobes, or very nearly so, 4 mm. long, four-seeded, the seeds 2.5 mm. long, rounded on the back, foveolate, the hollowed ventral side with a salient ridge lengthwise through the middle, the edges rounded.

I am indebted to Mr. J. Francis Macbride of the Gray Herbarium for the information that Mr. C. F. Baker's No. 758, collected at Ouray, Colorado, in 1901, is the original specimen from which *Phacelia Bakeri* (Brand) F. Macbr. was described. It is possible that *P. formosula* may be considered as closely related to *P. Bakeri*, which Dr. Rydberg has made a synonym of *P. glandulosa* Nutt., or may be it might be considered the same species. But *P. formosula* is a rather smaller plant, the leaves are smaller, the hispid pubescense is not so coarse, the calyx lobes are narrower, and the capsule is smaller and shorter pediceled. The difference is also notable in the character of the seeds. Dr. Gray, in the Synoptical Flora of North America, observed of the group in which *P. glandulosa* is placed, "seeds oblong or elliptical, flatter and thinner" than those of the group in which *P. crenulata* Torr. is placed, and it might be added that their edges are surrounded by a thin flat margin. *P. formosula* has "seeds with excavated ventral face divided by a salient ridge," and rounded edges, like those of *P. crenulata* or *P. corrugata* A. Nels., except that they are not corrugated on the edges. The seeds are like those of *P. splendens* Eastw., only smaller.

The only locality from which I have *P. formosula* is North Park, Colorado; and the type specimens were collected near Walden, along the road descending to the Michigan Creek, August 6, 1918, No. 5794.

3. **Oreocarya monosperma** sp. nov.

Biennial or short-lived perennial, stem single or several from the crown of the root, 2–3 dm. high, hispid with coarse spreading hairs and a finer pubescence beneath, branching from about the middle into a thyrsoid-paniculate inflorescense; lower leaves oblanceolate, obtuse, with the petiole 3–8 cm. long, about a cm. wide, becoming smaller upward, sessile, very hispid on both sides, the coarse hairs pustulate at base, a fine indument beneath; caylx lobes narrowly linear, in fruit becoming 8–9 mm. long, hispid and pubescent as the stem; corolla white, the tube the length of the calyx lobes, 4 mm. long, the anthers attached at the throat, filaments almost none; nutlets, only one maturing, ovate, margined, the margin upturned, slightly more than 3 mm. long, lightly cross-ridged, and tuberculate between the ridges.

Oreocarya monosperma in appearance is much like *O. thyrsiflora* Greene; the two plants are about the same size, but the thyrsus is not so long in comparison with the stem; the nutlets are darker in color, ridged more, and less tuberculate, one instead of four. Collected at Trinidad, Las Animas County, Colorado, July 20, 1918, No. 5754.

4. **Mertensia Clokeyi** sp. nov.

Stem slender, 2.5–3 dm. or occasionally 4 dm. high, glabrous or thinly appressed pubescent, branching from the upper third into a loose paniculate inflorescense, the peduncles often long and the flowers clustered at their ends; leaves rather remote on the stem, the lower narrowly linear, 3–4 cm. long, 3–4 mm. wide, the upper lanceolate, or narrowly ovate-lanceolate, acuminate, all sessile by a broad base, pubescent on both sides, the upper thinly with appressed, sharp pointed hairs, the lower less appressed; pedicels strigose pubescent, calyx 3.5 mm. long, the lobes 2.5 mm., lanceolate, glabrous, the edges ciliate; corolla 10–11 mm. long the tube half the length; filaments long, about the width of the anthers.

Mertensia Clokeyi was collected by Mr. Ira W. Clokey, of Denver, at Lake Eldora, Boulder County, Colorado, in woods, altitude 9,300 ft., No. 3161. It belongs to the *M. lanceolata* group. The leaves are pubescent on both sides, the pedicels strigose, and the calyx glabrous, except the ciliate edges of the lobes; in these respects it is like *Mertensia media* Osterhout, but the leaves are much broader and different in shape.

5. **Agoseris frondifera** sp. nov.

An acaulescent perennial, the scape occasionally bearing a leaf, and usually two large leafy bracts at the base of the involucre, 1–2 dm. high, glabrous except for the tomentum at the base of the involucre and some slight tomentum on the stem, mainly at the base; leaves narrowly oblanceolate, from 1 dm. to almost 2 dm. long, glabrous but not glaucous, entire or with several narrow lobes 1–2 cm. long; involucral bracts 2 cm. high, in three series, the inner narrow and scarious-margined, the outer broad, abruptly acuminate, longer and covering the inner, with a long tomentose pubescence especially on the margins; rays yellow; achenes striate for 8 mm., the beak 6 mm. long, the pappus white, 10 mm. long.

Agoseris frondifera is related to *A. montana* Osterhout; the bracts are like that species, and occasionally *A. montana* bears a leaf on the scape. It is in every way a smaller plant than *A. montana*, and the leaves are narrower. It was collected by Mr. Ira W. Clokey of Denver, as his label reads, at Camp Pitts, Boulder County, Colorado, in woods, altitude 9,600 ft., August 16, 1918, No. 3114.

6. ONOPORDUM TAURICUM Willd.

On July 22, 1918, I stopped for a few minutes at the Greenhorn Post Office in Pueblo County, Colorado, and across the road from the post office, growing in abundance along a little ravine was what I took to be some European *Cirsium*. The heads of purple flowers made an attractive showing. Mr. J. Francis Macbride of the Gray Herbarium identified it as *O. tauricum* Willd.

The sporadic appearance of non-edible mushrooms in cultures of Agaricus campestris

MICHAEL LEVINE

(WITH PLATES 3–5)

In studying the culture and development of *Agaricus campestris* during the winter and spring of 1916–1917, I visited some of the largest establishments of commercial mushroom growers in the East and thus have had an opportunity to study the fleshy fungi, other than the commercial varieties of *Agaricus campestris*, which appear sporadically in the mushroom beds. A number of such types for this country have been recorded by Peck* and others, The appearance, in the beds of one of the largest mushroom growers in New York City, of great numbers of *Panaeolus venenosus*, a very poisonous mushroom recently described as a new species by Murrill,† furnished material for the special study of its physiological and toxicological properties and I have published my results along this line elsewhere.‡ As this fungus seems quite dangerous I shall give here some results of observations made on the growth habits and describe another variety or form in which it sometimes occurs.

Panaeolus venenosus Murrill (PLATE 3, FIGS. 1–8).– This species is of interest to mycologists, since up to the present time it has been found only in two widely separated mushroom houses in the vicinity of New York City, in beds spawned for *Agaricus campestris*. The problem of its origin or occurrence in the wild state still remains unsolved. The plants studied were found in several different mushroom houses. In greenhouses which had been imperfectly darkened, better developed plants appeared, such as are shown in FIGS. 2 and 6. The plants grew in small fairy rings, mostly one to two feet in diameter, and in the darker mushroom houses were made conspicuous by the markedly developed white

* N. Y. State Mus. Bull. 157 67–68, 73. 1911; Bull. 150: 43. 1910.

† A very dangerous mushroom. Mycologia 8. 186, 187. 1916.

‡ The physiological properties of two species of poisonous mushrooms. Mem. Torrey Club 17: 176–201, *pl. 1, 2.* 1918.

tomentose bases of the stipes, as shown in FIG. 7. My observations as to the diagnostic characteristics of the fungus agree with the description given by Murrill. The spore print, however, although blackish in general, appears to have a delicate purplish hue. The shape of the spores is like that of the other species of *Panaeolus*. In my spore prints there is a great number of translucent, possibly immature spores. The following characters are generally present. The sporophores are 6–12 cm. tall; they are cespitose or gregarious. The pileus is 2–5 cm. in diameter and is rather fleshy. Its shape differs with the age, being campanulate in young specimens, later becoming plane and umbonate. The surface is moist and hygrophanous and is fulvous to isabelline in color (Ridgw.) when young, and dark bay when mature. In mature specimens the surface becomes wrinkled, as shown in FIG. 1. The gills are adnately attached and fuliginous in color with a grayish white edge. The stipe is fleshy, but hollow in the center, and in length is approximately two to three times the diameter of the pileus. The surface is striate and is covered with small hair-like scales. The base of the stipe is, as noted above, conspicuously covered with a white tomentum.

The obviously different looking plants, shown in PLATE 4, FIGS. 12–14, appeared during the month of April in one of the greenhouses in which the floor below the benches was used for mushroom culture. These plants were not abundant but were collected twice during the month. The whole of the material weighed about 40 grams, most of which was used in the experiment to determine the physiological and toxological properties. It was found that the plant was poisonous in the same degree as *P. venenosus*. The sporophores in general are like those of *P. venenosus* but they differ materially in the length of the stipe. The stipe is 2–4 cm. long and 5–8 mm. thick; that is, one fifth to one third the size of the stipe of *P. venenosus*. It is striate, however, and is somewhat covered with hair-like scales, as in *P. venenosus*. It is hollow and tapers slightly toward the base. Its color is fulvous and darker at the base than the stipe of *P. venenosus* and the tomentum at the base, noted in *P. venenosus*, is poorly developed and may be lacking. The taste and color are like those of *P. venenosus*. It may be regarded as a form of that species.

Panaeolus campanulatus L.,* which was the first member of this genus to be recognized as poisonous, also appeared in the mushroom beds. These plants appeared late, however, after the crop of *Agaricus campestris* mushroom was exhausted. The size and abundance of the sporophores might make them tempting to the uninitiated. The characteristics of the plants observed were identical with those already described for this species. The color of the pileus may be more accurately described as tilleul buff (Ridgw.) at the center and darker at the margin.

Panaeolus retirugis Fr. (PLATE 2, FIGS. 9–11) was also found in the beds mixed in with the sporophores of *Agaricus campestris.* It was the next most common to *P. venenosus.* A large number of these plants were collected during the month of April and they had been fairly common earlier. Species of *Panaeolus*† in general have been regarded as suspicious, especially *P. retirugis.* This plant was studied toxicologically by Ford and I have also found it to be poisonous to the same degree as *P. venenosus* when applied to the gastrocnemius muscle of the frog and the vagus nerves of frogs and turtles. The characters of the plant, as grown in dung-piles and well-manured lawns, are well known and the specimens collected by me were fairly typical.

The occurrence of *Panaeolus campanulatus* and *P. retirugis* in the mushroom beds may be accounted for by the coprophilous nature of these plants. It is possible that the mycelium of these species of *Panaeolus* are brought into the mushroom houses with the manure or introduced by flying spores in early autumn. The other possibility lies in the method employed for obtaining commercial spawn. It appears that some of the spawn makers in the eastern United States are following the method employed in England and France for obtaining a commercial spawn.‡ This consists of making trenches in the sod, where "spontaneous" mycelium or sporophores of *Agaricus campestris* appear in the

* See McIlvaine & Macadam. One thousand American Fungi 386. . 1900.

† See Krieger, C.C.L. Note on the reported poisonous properties of *Coprinus comatus.* Indiana. Mycologia 3: 200–202. 1911. Also Murrill, W. A. A new poisonous mushroom. Mycologia 1: 211–214. 1909.

‡ See Duggar, B. M. The cultivation of the mushroom. U. S. Dept. Agric. Farmers' Bull. 204; 1–25. 1911; The principle of mushroom growing and mushroom spawn making. U. S. Dept. Agr. Bur. Plant Ind. Bull. 85: 1–60. *pl. 1–7,* 1905; Mushroom growing 92. New York. 1915.

pasture, and filling them with thoroughly fermented manure. The vigorously growing mycelium spreads into this manure after several weeks. When this occurs, the manure is taken out of the trenches and slowly dried. This constitutes "virgin spawn," from which the commercial spawn is made. By this method it is conceivable that the mycelia of a number of fungi may be found growing in the "virgin spawn" and be propagated in the commercial spawn. This at least seems to be a plausible explanation for the introduction of *P. venenosus* into mushroom houses. This is supported by the fact that the fungus appeared only after the beds were spawned; as mentioned above it appeared in two widely separated mushroom establishments, both of which, however, were using the spawn from the same spawn maker. How *P. venenosus* escapes observation in the field is still a question that remains unsolved.

It is possible that the plant is a species of *Psilocybe* or *Inocybe* made aberrant by cultural conditions. Another possibility may be that the mycelium never has conditions in the open favorable to the development of sporophores but produces fruit bodies under cultivation only.

Clitocybe dealbata Sow. (PLATE 2, FIGS. 15–17). A species of *Clitocybe* which I have identified as belonging to the variable species known as *Clitocybe dealbata* also appeared. These plants were found in several mushroom houses in great abundance, growing in large clumps in the beds of *Agaricus campestris*. The *Clitocybe* species were found in these houses from January to May.

There are three recognized varieties of *Clitocybe dealbata* Sow., namely, var. *minor* Cooke, var. *deformata* Peck, and var. *sudorifica* Peck. The var. *sudorifica* was later made a species by Peck. The essential diagnostic characteristics of these plants, as given by Peck follow. *C. dealbata* has a white, fleshy pileus with a wavy margin; the gills are close, thin, adnate, and white in color; the stipe is fibrous, equal, and stuffed or hollow. Var. *minor* differs from the typical form of the species in its smaller and more regular form, its opaque gills, and the pleasant farinaceous odor. Var. *deformata* has a thin white, and very irregular pileus with a wavy or lobed margin; the gills are adnate or

slightly decurrent. *C. sudorifica* Peck has an irregularly shaped pileus which often becomes lobed; the gills are adnate and slightly decurrent; the pileus is watery when moist and whitish or grayish white when dry. This species was confused with *C. dealbata*, but the presence of sudorific properties forms a good basis for distinguishing them. The size of the spores in all these forms is approximately the same. While *C. dealbata* and its varieties are generally known to inhabit lawns and grassy places, the typical form of the species and the var. *deformata* have been reported growing in mushroom houses. As far as may be judged from the descriptions and the study of Peck's original herbarium material the species and varieties are separated only with great difficulty, yet I believe that the specimens I found are more like the typical *C. dealbata*, although I have not studied the toxicological properties of the juices of these various plants.

Ford* and his collaborators found that the juices of *C. sudorifica* were very toxic to guinea pigs and rabbits. Peck described earlier the sudorific effect induced by eating this plant. Gillot † and Clark and Smith ‡ have recognized and studied the poisonous properties of other species of the genus. In view of the toxic properties of the members of the genus the abundance of this species in a commercial mushroom house is of interest. As in the case of *Panaeolus* the species may have been introduced into mushroom houses through commercial spawn or flying spores.

Tricholoma melaleucum Quél. PLATE 5, FIGS. 21-23, shows a fungus which I found but once in the mushroom houses. The sporophores were discovered in an old mushroom bed. I am not altogether sure of its identity. There are slight discrepancies between my specimens and the description of this species given by Murrill§ (*Melanoleuca melaleuca*). These differences may perhaps be accounted for by the abnormal conditions under which

* Ford, W. W., & Sherrick, J. L. On the properties of several species of the Polyporaceae and a new variety of *Clitocybe*, *Clitocybe dealbata sudorifica* Pk. Jour. Pharm. and Exp. Ther. 2: 549–558. 1911; Further observations on Fungi, particularly *Clitocybe sudorifica* Pk., *Pholiota autumnalis* Pk. and *Inocybe decipiens* Bres. Jour. Pharm. and Exp. Ther. 4: 321–332. 1913.

† Etude médicale sur l'empoisonnement par les champignons. Lyon. 1900.

‡ Toxcological studies on the mushrooms *Clitocybe illudens* and *Inocybe infida*. Mycologia 5: 224–232. *pl. 91*. 1913.

§ N. Am. Fl. 10[2]: 7. 1914.

these plants grew. However, the description and published illustrations* of *Tricholoma melaleucum* best fit this plant. The sporophores I found are somewhat larger than the type described by Murrill, whose herbarium material I compared with my plants. The pileus is larger than this type and measures 3–9 cm. in diameter, while in height the plant agrees with the description. The pileus is thin, convex to plane and depressed. The margin is lobed and may become divided into a number of segments as shown in FIG. 23. The color of the pileusis drab to light drab (Ridgw.). The gills in these specimens were not very white, as described by Murrill, but drab gray. The spores of this plant agree perfectly with those of *T. melaleucum*. The stipe is even, although it may be enlarged at the top and at the base. The surface is reticulately veined as shown in FIG. 21 and in this respect is unlike the description. Its color agrees with the description. Up to the present *T. melaleucum* has been reported as found only in woods, fields and lawns. Its habit is solitary and the plants found in the mushroom beds were solitary, although they tended to be cespitose.

Peziza domiciliana Cooke† (PLATES 4, FIGS. 18–20). The *Peziza* shown in FIGS. 18–20 is common in all the mushroom houses studied. It makes its appearance as early as November and can also be found late in the spring. The plants generally appeared before and during the growth of the mushrooms. I am indebted to Dr. Seaver for the identification. While the plants agree in the main with the description given for *P. domiciliana*, there are some differences. The apothecia grow singly or gregariously but never caespitose. The outer surface of the cup has a white granular appearance and the color of the hymenium is pale ochraceous salmon (Ridgw.) when young, to Dresden brown, when old, instead of ochraceous buff or dungy buff as given by Overholtz and Seaver. While the spores are ellipsoidal and hyaline when young, and in this agree with the description already published, they are slightly smaller in size.

A considerable number of species of *Coprinus* appeared in the

* See Barla. Les champignous des Alpes-Maritimes *pl. 46, f. 8–15*. 1888.

† See Seaver, F. J. Development of the cup Fungi. Mycologia 8: 195–198. *pl. 188, 189*. 1916.

compost after the beds were made and several species of *Poria* were found on the wooden framework in some of the more moist houses, but I shall not report on them at this time.

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Description of plates 3-5.

In PLATES 3 and 5 the natural sizes of the plants are represented; in PLATE 4 the figures are slightly reduced.

PLATE 3

FIGS. 1–4. Young stages in the development of *Panaeolus venenosus* Murrill.

FIGS. 5–8. Mature stages of *Panaeolus venenosus*.

FIGS. 9–11. Stages in the development of *Panaeolus retirugis* Fr.

PLATE 4

FIG. 12. Longitudinal section of a mature carpophore of *Panaeolus venenosus* with a short stipe.

FIG. 13. Young carpophore of *Panaeolus venenosus* with a short stipe.

FIG. 14. The under surface of the pileus of *Panaeolus venenosus* with a short stipe.

FIGS. 15–17. Clusters of *Clitocybe dealbata* Sow., showing the upper and lower surfaces of the pilei.

FIGS. 18–20. Mature stages in the development of *Peziza domiciliana* Cooke.

PLATE 5

FIGS. 21–23. Different stages of a fungus that most closely resembles *Tricholoma melaleucum* Quél.

INDEX TO AMERICAN BOTANICAL LITERATURE

1911–1918

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word Amer ica being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

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Gametogenesis and fecundation in Zea Mays as the basis of xenia and heredity in the endosperm

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(WITH PLATES 6 AND 7 AND TWO TEXT FIGURES)

In the almost endless number of varieties of maize there is afforded excellent material for experimental work on heredity, as is indicated by the part that the plant has played in the genetic studies of the past twenty years; but, unfortunately, maize offers at the same time limited opportunity for satisfactory cytological work. In addition to its other advantages, maize has a variable endosperm, in the transmission of whose characteristics we get not only a deeper insight into the true nature of the angiosperm endosperm but also some interesting checks on general theories of heredity. But many of the conclusions drawn from these endosperm studies have been based upon the assumption of certain facts concerning gametophyte development and a single description of the fecundation process, of which no figures were given. It was for the purpose of putting the cytological side of the question upon a substantial basis that this study was undertaken. The structure and development of the spikelets have been described in other papers (23, 24), and only the essential details will be repeated.

THE MEGASPORE

Before the integuments have made any considerable progress in enclosing the nucellus, the archesporium becomes visible as a

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large hypodermal cell near the tip of the nucellus (PLATE 6, FIG. 1). It soon divides periclinally, giving rise to a parietal cell, the tapetum, and a megaspore mother-cell; but no wall is formed, and the tapetal cell is immediately consumed (FIG. 2). The parietal layer of tissue, five to eight layers of cells in thickness, which is ultimately present (FIG. 16), is formed from epidermal cells by periclinal divisions (FIG. 2 and TEXT-FIG. 1).

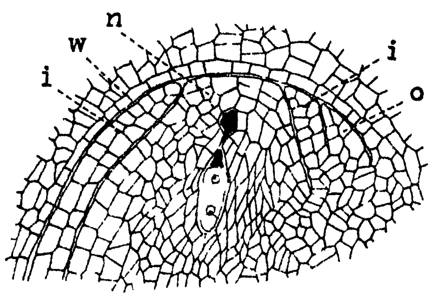

FIG. 1. Binucleate stage of megaspore germination, to show surrounding tissues, × 220: *ii*, inner integument; *o*, outer integument; *w*, ovary wall; *n*, tip of nucellus.

In another connection (24, p. 492) the statement was made that, inasmuch as no evidence had been seen of the disorganization of any of the megaspores, all four probably functioned as in the lilies. But it has since been pointed out to me by Mr. E. G. Anderson, of Cornell University, that, if such be the case, the results of certain experiments on heredity in the endosperm must receive a new interpretation. Consequently, a thorough investigation of the development of the megaspore and embryo sac was thought profitable.

The heterotypic division of the mother-cell is, in all essential details, similar to that in other plants (FIGS. 3, 4). The chromosomes are small and the karyokinetic figures indistinct; and the material is not satisfactory for giving any light on controverted questions of cytology in general. The bivalent character of the chromosomes at this stage is, however, beyond question. A wall is laid down between the two cells resulting from this division (FIG. 5).

The more deeply-seated of these two cells next divides, giving rise to two megaspores (FIG. 6). The other cell begins to divide, but the process is arrested, usually at about the spindle stage, by the incipient disintegration of the dividing cell and the adjacent megaspore (FIG. 7). Thus, only the chalazal one of the four megaspore potentialities persists (FIG. 8). The absorption of the other three is not completed until the embryo sac is almost mature (FIGS. 8–12).

THE EMBRYO SAC

The germination of the megaspore is the same as that in most plants where an ordinary seven-celled embryo sac is to be formed. In the two-nucleate stage (FIG. 9) there appears a large central vacuole, accompanied by a smaller one at the chalazal end of the cell; these vacuoles persist through subsequent stages until the ultimate organization of the embryo sac. The position of the spindles following the four-nucleate stage (FIG. 11) and the arrangement of the following eight nuclei (FIG. 12) substantiates the observation made on numerous other plants that one of the polar nuclei is the sister of the egg.

When the membranes are first formed (FIG. 12), dividing the gametophyte into cells, the antipodals are much larger than the cells of the egg apparatus; but, by the time the embryo sac is fully organized (PLATE 7, FIG. 13), the egg and the synergids have greatly enlarged, and, with little or no increase in size, the antipodal cells have begun to divide, forming the multicellular antipodal tissue which seems to characterize the embryo sacs of most grasses. Meanwhile, the polar nuclei have come together near, or in contact with, the plasma membrane of the egg.

After its organization, the embryo sac continues to increase in size, at the expense of the nucellus, until, at the time of fecundation, it has a volume five to ten times as large as it had at the eight-nucleate stage. This growth is accompanied by rapid changes in other parts of the pistil as well. The nucellus grows rapidly and pushes the integuments out against the ovary wall, which, growing less rapidly, is kept tightly stretched over the turgid ovule. The style, or "silk," increases from a length of one or two centimeters to its full length, which may be forty centimeters or more in some varieties, and develops its numerous stigma hairs.

Guignard (10, p. 44) has given a good description of the embryo sac. It occupies relatively a very small part of the nucellus (TEXT FIG. 2). The cells of the egg apparatus are very large (FIGS. 13, 16). The dense cytoplasm of the pear-shaped synergids shows the longitudinal striations characteristic of these cells in many other plants. The nuclei are located well toward the micropylar ends of the cells and react so feebly to stains as often to be indistinguishable. The egg is larger and more rounded than a

synergid, and its cytoplasm is much less dense. The nucleus is almost centrally located and is closely surrounded by most of the cytoplasm of the cell. It is a little larger than that of a synergid and always stands out distinctly; the nucleolus is large, but the chromatin granules are small and scattered.

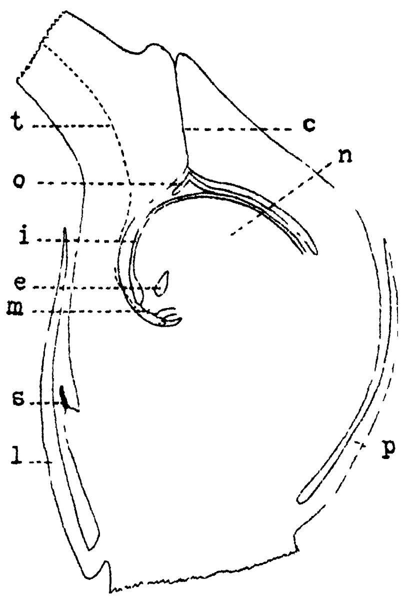

FIG. 2. Longitudinal section of female floret, for purpose of orientation, × 75: *l*, lemma; *p*, palea; *e*, embryo sac; *n*, nucellus; *o*, outer integument; *i*, inner integument; *m*, micropyle; *c*, stylar canal; *t*, course of pollen tube after reaching the ovary; *s*, rudimentary stamen.

The polar nuclei resemble the egg nucleus but are often a little larger. They are usually surrounded by a dense mass of cytoplasm, which often makes detailed observation difficult. They do not fuse until after the entrance of the pollen tube to the embryo sac, even though pollination be artificially delayed until long after the normal time.

The antipodal tissue continues to grow until the time of fecundation, often consisting of fifty or more cells, some of which may have more than one nucleus. A number of these have been observed in the process of division, and, while accurate counts of the chromosomes have not been made, there is nothing in the appearance of the karyokinetic figures to indicate that there are any more than the haploid number as has been reported for many other plants. The theoretical significance of this antipodal tissue in the grasses has never been fully investigated, and it may help some time to explain the female gametophyte of the angiosperms. It is probably the equivalent of the endosperm of gymnosperms, but in maize it is completely absorbed soon after fecundation and never becomes a part of the endosperm of the mature seed.

THE POLLEN TUBE

As has already been noted (**24**, p. 487), the generative cell of the pollen grain has divided, forming two very small, crescent-shaped sperms, before the dehiscence of the anther. The pollen grain finally comes to rest on the silk where it is probably held by some sticky exudation that may be instrumental in initiating germination. The pollen tube emerges very soon and makes its way down through one of the stigma hairs to the body of the silk (FIG. 14). Here it pushes its way between the parenchyma cells, absorbing food from them, no doubt, until it reaches one of the vascular bundles, which it follows toward the ovary.

At the time of its emergence from the pollen grain, the tube is greatly exposed to desiccation, and this continues until it has made its way into the body of the silk. This, together with the fact that the pollen grains themselves dry up very readily and are seldom viable for more than a day or two, probably accounts for the importance to the corn crop of warm rains at the time of pollination.

In some kinds of corn the silks may attain a length of fifty centimeters or more, and there are probably few species of plants in which the pollen tube has farther to grow. Consequently, it has been an interesting problem to determine the time elapsing between pollination and fecundation. A number of experiments were made to determine this, and the best results were obtained with a small variety of sweet corn with silks about twenty-five centimeters in length. Silks that had been properly protected were pollenized at 2:45 P.M. on a warm, foggy day in early September, with pollen that had been shed on the forenoon of the same day, and ovules and segments of silks were fixed at various intervals for two or three days after pollination. It was found that within two hours the pollen tubes were well established in the silks. This result has also been verified by several experiments in the laboratory (FIG. 14). Ovules fixed twenty-five hours after pollination showed fecundation and stages just before (FIG. 16) and just after fecundation. These results could, of course, be modified by extensive experiments with silks of different lengths and pollen of different ages and at different temperatures, degrees of humidity, etc., but that is rather the problem of the physiologist.

The aim in presenting here the meager data available is to show the great rapidity with which the pollen tube grows. It is interesting to note that Jensen (13, p. 15) finds a somewhat greater time (32 to 40 hours) between pollination and fecundation in wheat, although the style of the latter is much shorter than in maize.

It is not to be inferred that there is at any one time a living pollen tube reaching from the stigma hair to the embryo sac; and this statement is probably very generally true of all angiosperms. Observation of the pollen tube in the silk is difficult, but it is probable that there is not more than a centimeter or two of it alive at any one time; and the living portion seems to become shorter and broader as it approaches the ovule. It is in most cases practically impossible to find any trace of the pollen tube in the tissue through which it has passed.

One of the difficulties in attempting to observe fecundation is in being able to identify the sperms when they reach the embryo sac. The protoplasm of the pollen tube, as it grows down through the silk, is so dense and so coarsely granular that it is almost impossible to distinguish with certainty the sperms and the tube nucleus. Both can be made out with a fair degree of certainty, however, in the less dense contents of the tube in the ovary cavity as it approaches the embryo sac; and they are, of course, visible in the pollen grain before germination. The tube nucleus is irregular in size and shape and does not seem to have a definite membrane. There is no visible difference between the two sperms. They are very small, slender crescents, with the ends drawn out to very fine points (FIGS. 15, 16). The nucleus, which seems to consist almost wholly of chromatin, constitutes the greater part of the cell and forms the middle of the crescent; no nucleolus has been observed. There is only a small quantity of cytoplasm, and nothing of its details can be made out.

The size of the sperm is remarkably correlated with the long distance through which it must be carried from the pollen grain to the embryo sac. Practically all varieties of maize are fertile *inter se;* and this means that any pollen grain, even though it be produced by a plant characterized by short silks, is capable of producing a pollen tube as long as is necessary, as is determined by the length of the silk of the variety pollenized.

The path of the pollen tube on reaching the ovary has never been satisfactorily explained. True (20, p. 217) quotes Hackel (11) as saying that the outer integument acts as a conducting tissue. Guignard (10, p. 43) says that the tube enters the ovary by way of the stylar canal. My preparations have not given conclusive results, but they do not tend to substantiate these opinions. The pollen tube seems to grow downward from the base of the style until it reaches the inner epidermis of the wall of the ovary (TEXT FIG. 2). Remnants of it can be traced just below the epidermis to a point near the micropyle, where it enters the ovarian cavity. After following a very crooked course here, it finally enters the micropyle, forces its way between the cells of the parietal tissue, and enters the embryo sac (FIG. 16).

FECUNDATION

The contents of the pollen tube may be emptied between the cells of the egg apparatus or into any one of them; but it is usually emptied into a synergid. The membrane of the other synergid often seems to break at about the same time, emptying its contents into the cavity of the endosperm cell. The tube nucleus is soon lost to view, if it was visible at all; and, because of their extremely diminutive size, it is very difficult to follow the sperms beyond this point. The cytoplasm of the area to be examined is very dense and is filled with numerous globules of various sizes and shapes (FIGS. 13, 16), produced, no doubt, by the mixing of the cell contents brought together by the entrance of the pollen tube. The disorganizing synergids give rise to cytoplasmic differentiations that are especially confusing. Material fixed with reagents containing osmic acid presents almost hopeless complications; but, with chromo-acetic acid as a fixing agent, followed by Flemming's triple stain, the sperm nuclei can be identified.

In several preparations a small red object, which is like a sperm nucleus in size, shape, and granular appearance, has been seen sticking to the egg nucleus (FIG. 17); and a similar body has, in a number of instances, been seen attached to one (FIG. 18) or both (FIG. 19) of the polar nuclei, which were in the process of fusion. No fusing polar nuclei have been seen without this sperm-like body. On this basis, then, it seems certain that the so-called "double fecundation" takes place in maize

In 1901 Guignard (10) reported having observed this process, but his otherwise excellent paper was not illustrated. While his results have been generally accepted by morphologists, and made the basis of extensive work by geneticists, the desirability of a verification is attested by the number of students who are known to have attempted at different times to repeat his work. If negative results were generally published, we should, no doubt, have a much more voluminous literature on this point.

In one preparation the writer observed the two fusions taking place simultaneously (FIGS. 17, 18), but in a majority of cases one preceded the other. Whether or not there is a definite order in which the fusions occur has not been determined, because it is almost impossible to determine by appearance alone whether a cell under observation is an egg or a zygote. It is true in all cases, however, that several free endosperm nuclei are formed before the first division of the fecundated egg.

At the time of fecundation the egg nucleus is often seen to have moved to one side of the cell (FIG. 16), and the polar nuclei may also migrate within a limited range, often approaching the micropylar end of the embryo sac. Whether or not there is any significance to be attached to these migrations has not been determined.

These fusions take place while the egg nucleus and the polar nuclei are in a resting condition (FIGS. 17–19). The chromatin is gathered into numerous round, globular bodies, some of them almost as large as a sperm; and these granules are loosely connected by strands composed of finer granules of similar appearance. That these chromatin bodies are not the "prochromosomes" of some authorities is attested by their number, which is far too great.

XENIA

As long as maize has been cultivated, it has been noted that, when white and colored varieties of some kinds were grown close together, the ears of the former were likely to bear a few colored seeds. The American Indians are said to have observed this and to have attributed it to the intermingling of the roots underground. Later, civilized man attributed the phenomenon to some effect of cross pollination, but its mechanism long remained a mystery.

In 1881, Focke (9, p. 511) coined the word *xenia* to apply to the immediate effect of foreign pollen upon maternal tissue.

Nawaschin's discovery (16) that in many plants, one of the sperm nuclei enters into the makeup of the endosperm, suggested an explanation of the mechanism of xenia in maize; and Guignard's discovery of "double fecundation" in maize, in 1901 (10), left no room for reasonable doubt as to the mechanism of xenia.

The immediate effects of cross pollination, that is, such effects as may immediately be observed in the seed or fruit in which the hybrid embryo is borne, are probably not so common as has often been supposed; and by no means are all of them illustrations of xenia, in the true sense of the word.

There is a common belief that pumpkins growing near watermelons will, by hybridization, impair the quality of the latter in the first generation; and numerous other instances have been cited of slight changes in the quality of fruits, supposed to be due to the immediate effects of cross pollination. The experimental demonstration of most of these, with races known to be genetically pure for the characteristics considered, has not been accomplished.

Another type of the phenomenon is afforded by hybrids between varieties of peas and other plants, which are variable as to the color or physical character of the cotyledons. Here a dominant character may, through hybridization, appear in seeds borne on plants pure for the recessive character. But this is merely the early recognition of a hybrid by means of characteristics that are differentiated in the embryo. Bailey and Gilbert (1) must have had in mind such phenomena as these when they made the erroneous statement (p. 327) that xenia occurred in peas.

In contrast with these phenomena is the immediate effect upon the endosperm, so well known in maize. This has also been demonstrated in teosinte-maize hybrids (21), and has been reported in a few other crosses between different varieties of cereals. The primary essential for xenia is *variability of endosperm* in plants that will hybridize, and for this reason, maize when used for one of the parents, at least, furnishes the best-known illustration.

In a recent review of the whole question of influences following fecundation, Waller (22) suggests that the term *xenia* be reserved for the phenomenon limited to the endosperm of angiosperms and

due to the entrance of a sperm into the constitution of the primary endosperm nucleus. It is a direct result of the introduction of hereditary factors into the endosperm and not to be attributed to enzymatic action or other stimulating influence. To include "those influences which follow fertilization but are remote from it" (p. 282) and are "due to the developing zygote" (p. 284), he proposes the term *ectogony.*

Whether or not the new term is applicable, is not a question to be decided in this connection; but the distinction between xenia and other influences less directly connected with fecundation is a timely one. Xenia may be defined, then, as *any effect that may be produced upon the endosperm of an angiosperm by pollination with pollen from a plant having a different kind of endosperm.*

Of course, it is not to be expected that xenia will occur in all such crosses. Correns (3, pp. 411–414) has outlined a number of cases in which xenia will or will not occur in maize, and East and Hayes (7, p. 103) have condensed all the available data into a law of xenia. For our purpose, it may be said that xenia will occur in any cross in which the male parent possesses the dominant and the female the recessive of an allelomorphic pair of endosperm characters, or when the two parents possess respectively two characters whose interaction is necessary for the production of a visible effect. When dominance is incomplete, or when inhibiting factors are present, complications are introduced which need not be discussed here.

THE ENDOSPERM OF ANGIOSPERMS

The variability of the maize endosperm, with the accompanying phenomenon of xenia, gives it a prominent place in any explanation of the endosperm of angiosperms. This tissue has been explained in many ways, but its true significance still offers an unsolved problem. The correct explanation, if it is ever found, will probably develop from researches on the phylogenetic origin of the angiosperms.

In most of the plants in which fecundation has been studied, one sperm has been found to enter into the constitution of the endosperm, and the phenomenon is believed to be of general occurrence. But there are many exceptions which serve to com-

plicate the problem. A good résumé if these is given by Coulter and Chamberlain (5, pp. 165–186), and more are being added from time to time.

Miss Sargant (17, p. 702) stated clearly the problems involved in the interpretation of the triple fusion and reviewed the explanations that had been given up to 1900. Although her paper appeared very early in the investigation of the question from the modern point of view, it showed such a clear insight into the nature of the problem that the data that have accumulated since that time have afforded little foundation for further constructive work.

Some have considered the endosperm merely a belated prothallium, the triple fusion of nuclei being non-sexual and of no more significance than the nuclear fusions that often occur in vegetative tissue. Strasburger (18, p. 308) calls the triple fusion a "vegetative fertilization," as contrasted with the "generative fertilization" of the egg. These types of fecundation resemble each other in the transmission of certain hereditary characters, but they differ in the nature of the new individuals produced.

Again (17, pp. 704–706), the endosperm may be looked upon as a monstrous embryo, its aberrant nature and limited development being determined by the antipodal one of the polar nuclei, inasmuch as its chromosome number is known to be irregular in many plants. According to this view, the endosperm is neither sporophyte nor gametophyte, but a new generation, characteristic of the angiosperms alone, and for which Trelease (19) has proposed the name *xeniophyte*, because it is the generation in which xenia may occur.

All agree upon the function of the endosperm as an organ of nourishment for the embryo, and its rapid growth has been attributed to its sexual, or pseudo-sexual, origin. Collins and Kempton (2) and Jones (14) have even shown that hybrid endosperms, produced by crossing varieties of maize that have been selfed for some time, show a perceptible increase in size over those of the parent races. This is attributed to the increased vigor usually resulting from hybridization. Miss Sargant (17, pp. 709–710) has suggested that the introduction of the paternal elements into the primary endosperm nucleus may be a device of the plant to pro-

duce a food of proper quality for the hybrid embryo. In the light of later work on xenia, we should be compelled to infer from this that the peculiar endosperm qualities necessary in such cases were the *dominant* characters, since we have no evidence that, except in special cases to be mentioned later, the recessive characters of the male are ever effective in the endosperm; they are not visible, and there is no future generation in which they might be detected. Moreover, in a cross between sweet and starchy varieties, the former being the female, there is produced a starchy endosperm, which is harder to digest than the sweet one that would have been produced had the triple fusion not occurred.

The part played by the maize endosperm, then, is to complicate the problem and at the same time act as a check on our solutions. Were it not for xenia and the attendant hereditary phenomena, the logical disposal of the endosperm would be to call it gametophytic tissue resulting from a triple vegetative fusion to which no great significance could be attached; and this would probably have been done long ago had the peculiarities of the maize endosperm not been known. But the transmission of hereditary characters to this tissue, as illustrated in maize and a few other species, strongly suggests its parallelism with the sporophyte and saves us from an incorrect explanation of the ques ion.

HEREDITY OF ENDOSPERM CHARACTERS

Without committing ourselves as to the most logical interpretation of the endosperm in general, we may, for the purpose of explaining genetic data, adopt the convenient expedient of considering the endosperm of maize a monstrous sporophyte, a sort of sister of the embryo. It derives a vigorous growth stimulus from the triple fusion in which it originates. It passes through a series of tissue differentiations, none of which, however, resemble very closely those characteristic of the embryo. It never reaches sexual maturity, and, consequently, has no descendants. Because of the sporophytic nature of the endosperm, Mendelian principles of heredity have been applied to its study in maize, with results unique in many instances, and all dependent, more or less, upon the cytological facts here set forth, or, at any rate, nor at variance with them.

The maize endosperm is either sweet or starchy. The starchy tissue occurs in two forms, one corneous and translucent, and the other soft and white; and different proportions and variations in the arrangement of the soft and corneous portions gives rise to dent, flint, pop, and soft types. The mature seeds of the sweet varieties are always wrinkled; they are to be understood as having pop, dent, flint, and soft potentialities remaining invisible because of limited starch development. The starchy condition is dominant to the non-starchy, but dominance among the variations of the starchy condition is a less definite thing.

The corneous endosperm is either white or yellow; the yellow color, which has been found to be due to more than one hereditary factor, is dominant. It may appear in either the starchy or the sweet endosperm.

The aleurone is red, purple, or colorless. Two hereditary factors are necessary for the production of the red color, and these, interacting with a third, produce purple. The presence of either color combination is dominant to its absence, but other color genes are also present, at least one of which is an inhibiting factor.

Correns found (**4**) in certain crosses that a white variety pollenized with pollen from a purple did not always produce purple aleurone, although the embryos of the same seeds proved to be hybrids. He explained this non-appearance of xenia by assuming that the recessive factors carried by the two maternal nuclei entering into the primary endosperm nucleus were dominant over the one factor introduced by the sperm, although the latter was ordinarily dominant.

East and Hayes (**7**, pp. 58–59), having found a better explanation of this aberrant result, attacked Correns's hypothesis on the ground that quality and not quantity of chrómatin is the determining factor. In this argument they failed to distinguish between the idea of double quantity and quality acting twice.

In later experiments (**12**, p. 12) they found that when reciprocal crosses were made between a soft and a corneous variety, the quality of the endosperm produced was always determined by the female parent. At the same time it was shown that a soft white female crossed with a flinty yellow male produced soft yellow seeds. The appearance of xenia in color showed that the peculiar

results of the reciprocal crosses were not due to a failure of the sperm to fuse with the polar nuclei, as Webber had suggested (25, pp. 34–37) in explanation of a similar occurrence. Therefore, they were forced to conclude that two applications of the one factor may dominate one application of the other.

Results leading to the same conclusions have since been secured with color combinations. If a plant heterozygous for purple aleurone be selfed, four types of endosperm should be produced, depending upon the number of times the factor combination for purple is present. And when such an experiment is made, there are produced, besides the proper number of white seeds, visibly different types of purples, appearing in significant ratios. Emerson (8) has recently given a detailed report on a number of experiments of this kind.

It may be said, therefore, that the solution proposed by Correns was a valid one, although it did not apply to the problem that he had in hand. By taking advantage of the triple parentage of the endosperm, this series of experiments provided the first direct evidence of the cumulative effect of repeated applications of the same factor, which is the basis of the multiple factor hypothesis.

But these theoretical conclusions have all been based upon the assumption of certain cytological facts not hitherto demonstrated. If, in the formation of the maize embryo sac, all four megaspores functioned, which the writer (24, p. 492) at one time thought probable, the two polar nuclei, coming respectively from the two nuclei resulting from the heterotypic division, would be genetically different in a hybrid plant. Therefore, a sweet-starchy hybrid, crossed with pure sweet, should produce all starchy seeds, since the two polar nuclei together would represent an entity unaffected by segregation and always carrying the dominant factor. But, as a matter of fact, when a cross of this kind is made, a 1 : 1 ratio is produced. The assumption that only one megaspore survived had good precedent in Koernicke's work (15) on *Triticum*, recently verified by Jensen (13); but now it is definitely known that the same is true of maize.

In some crosses of white varieties with purple or red, a mottled aleurone is produced; and in sweet-strachy crosses a few seeds have been found with the endosperm bilaterally divided—one

half starchy and one half sweet. Webber (25, pp. 34-37) found an explanation for such irregularities in the assumption that the sperm might sometimes fail to fuse with the polar nuclei, and thus be left to divide independently, or might fuse with only one of them, the other dividing independently. In either case there would be two, possibly genetically different, sources of endosperm formation, which might account for the two colors of aleurone. It has since been found that aleurone mosaics are amenable to Mendelian principles, but for the divided endosperms East and Hayes (7, pp. 34-35) consider Correns's explanation well-founded.

This assumption requires that either the sperm or one of the polar nuclei, both of which have been considered gametic in nature, develop without uniting with another gamete, which would be a very unusual behavior. If such an explanation of the occurrence is necessary, it seems more reasonable to suppose that the sperm united with the polar nucleus coming from the micropylar end of the embryo sac, since it is the sister of the egg and necessarily much like a gamete, and that the antipodal one of the polar nuclei, with its possibly irregular chromatin organization, divided independently, as its near relatives, the true antipodals, regularly do in maize and other grasses. Yet this would take from one polar nucleus much of its gamete-like nature and might seriously interfere with its ability to transmit hereditary characters in the orthodox fashion necessary for some of the other phases of our theory. In fact, any assumption of this kind will lead to the conclusion that something, elsewhere considered gametophyte, here contributes directly to endosperm formation and shows endosperm (xeniophyte) characteristics.

The responsibility for these rare occurrences of bilaterally differentiated seeds may be placed upon still another hypothesis which involves valid cytology and is not in conflict with Mendelism. The division of the primary endosperm nucleus may be heterotypic in a way. In fact, it is well known that the subsequent divisions often show fewer than $3x$ chromosomes; some chromosomes must, therefore, at some time, pass bodily to the poles of the spindle without themselves dividing, and, if one of these carries the gene for starchiness, reduction necessitates a sort of Mendelian segregation.

In the frequency with which these bilaterally differentiated endosperms occur—about one in 10,000—East (6, p. 220) has likened them to "bud sports." This explanation is not materially different from the one suggested above, although the cytologica phenomena accompanying the formation of "bud sports" are not well understood at present. In the endosperm, where chromatin behavior seems much less regular than in ordinary embryonic tissue, the chances for such occurrence seem exceptionally good; but, neither in the division of the primary endosperm nucleus nor in the arrangement of the free nuclei in subsequent stages, is there anything to account for the perfect symmetry and fine line of demarcation characterizing these seeds.

SUMMARY

Of the four potential megaspores in maize, only one persists and becomes functional.

The embryo sac is a modified form of the ordinary seven-celled type. The antipodals undergo division, forming a large mass of tissue before the time of fecundation.

The sperms, which are exceedingly small, are matured inside the pollen grain before the dehiscence of the anther.

External conditions and the length of the silk determine the time required for the growth of the pollen tube, but fecundation is known to have taken place in some instances within a little more than twenty-four hours after pollination.

Guignard's work on double fecundation in maize is verified. Both sperms are functional, one uniting with the egg to give rise to the embryo, and the other entering into the constitution of the primary endosperm nucleus. This is the cytological basis of xenia and the attendant hereditary phenomena. Immediate effects of pollination made manifest outside the embryo, if such really occur, should not be called xenia.

The triple fusion takes place almost simultaneously with fecundation of the egg, but the endosperm develops much more rapidly than the embryo.

In connection with genetic studies, the assumption that the endosperm is sporophytic in its genetic behavior seems consistent. The cytological data substantiate practically all the assumptions

of cytological fact upon which recent experiments on endosperm heredity in maize have been based.

I take opportunity here to express my obligations to Professor D. M. Mottier for the suggestion of this problem and for valuable assistance and criticism in connection with the study.

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Explanation of plates 6 and 7

PLATE 6

All figures × 725

FIG. 1. The archesporial cell.

FIG. 2. Megaspore mother-cell and disorganized tapetal cell.

FIG. 3. Megaspore mother-cell in synapsis.

FIG. 4. Heterotypic spindle.

FIG. 5. Daughter cells resulting from reduction division.

FIG. 6. Two megaspores, *ss*, and micropylar daughter cell in process of division.

FIG. 7. Dividing daughter cell and one megaspore beginning to disintegrate: *s*, functional megaspore.

FIG. 8. Functional megaspore absorbing the other three.

FIGS. 9–12. Steps in the germination of the megaspore and organization of the embryo sac: *ss*, synergids; *e*, egg nucleus; *pp*, polar nuclei; *a*, antipodal cells.

PLATE 7

FIG. 13. Embryo sac soon after organization, × 725: *ss*, synergids (position shown by dotted lines); *e*, egg nucleus; *p*, polar nuclei; *a*, antipodal tissue.

FIG. 14. Germinating pollen grain on stigma hairs, × 200.

FIG. 15. Sperm, × 1750.

FIG. 16. Pollen tube entering embryo sac, × 385: *o*, outer integument; *ii*, inner integument; *t*, pollen tube; *w*, ovary wall; *s*, sperms; *n*, tube nucleus (probably); *e*, egg nucleus; *p*, polar nuclei in contact; *a*, one synergid; other synergid not shown.

FIG. 17. Sperm nucleus, *s*, in contact with egg nucleus, × 1500.

FIGS. 18, 19. Sperm nuclei, *ss*, in contact with the fusing polar nuclei, × 1500.

The effect of soaking in water and of aëration on the growth of Zea Mays

F. M. Andrews and C. C. Beals

(WITH FIVE TEXT FIGURES)

The first of these experiments was to ascertain the best length of time required to soak the grains of *Zea Mays* for growth to begin. The grains we used were one year old. Some experiments of this kind have been made,* but since the time varies to some extent in the grains of *Zea Mays* of different kinds and ages, it was desired to determine it for the material at our disposal. The second object was to determine the effects of aëration on the seedlings of *Zea Mays* under different conditions.

1. Experiments in soaking grains of Zea Mays

a. *Time required for maximum growth*

In order to ascertain the proper length of time to soak *Zea Mays* for maximum growth the grains were kept in tap water for varying lengths of time, and then in wet sawdust long enough to total forty-eight hours. The experiments were kept under normal growing conditions.

Tables I–IV give the average length of growth of five grains. The unsoaked grain used as a control made no external growth in any of the experiments.

TABLE I

Hours soaked	Growth in mm.
16	8.6
17	10.8
19	12.6
21	10.2
23	4.6
25	3.0

TABLE II

Hours soaked	Growth in mm.
6	5.2
8	11.2
10	11.5
12	13.4
14	11.6
24	4.8

* See Burt, G. J., Biggar, H. H., & Trout, C. E. The rag-doll seed tester. U. S. Dept. Agr. Farm. Bull. 948: 1–7. *f. 1–5.* 1918. On page 4 the writers state, "it is best not to soak for more than 10 hours." We have found, however, that 12 hours is the optimum length of time with our material.

TABLE III

Hours soaked	Growth in mm.
12	26.6
15	20.4
17.5	15.4
20.5	7 2
22.5	10.2

TABLE IV

Hours soaked	Growth in mm.
1.25	0.6
3.25	2.4
5.5	4.6

The results of the above series show that the amount of time for soaking the grains of *Zea Mays* for good growth ranges from about 8–14 hours with the optimum length of time near 12 hours. The series shown in TABLE I, however, indicates 17–21 hours as the best, but this discrepancy was due to a variation in temperature.

b. *Growth in sawdust and soil compared*

It is interesting to note the effect of the use of damp sawdust to germinate *Zea Mays*, as compared with damp soil. TABLE V gives the results with using grains soaked 11 hours in tap water and remaining in the soil (or sawdust) for 37 hours longer.

TABLE V

	Unsoaked Seed	Soaked Seed
Soil	8 mm. (av.* of 24 grains)	9.4 mm. (av. of 22 grains)
Sawdust	3.1 mm. (av. of 26 grains)	9.3 mm. (av. of 25 grains)

The soaked grains showed a difference of 0.1 mm. in favor of the soil; while the unsoaked grains in the soil showed a gain of 258 per cent in favor of the soil. That was due probably to the sawdust having a greater tendency to dry out than the soil. The grains probably absorbed the moisture more readily from the soil as its particles were smaller, thus tending to establish a better condition for absorption.

c. *Effect of puncturing the coats of the grains*

The large end of the grain was punctured, after which it was soaked for 10.25 hours and left in sawdust long enough to make 48 hours. The average growth of 25 punctured grains was only 11.7 mm., due to air which was engulfed or held for a long time in the small opening made by the puncture; 11 had a growth of 10 mm. or more; 7 with a growth of less than 10 mm., and 7 without

* "Av.," wherever used in this paper, stands for "average."

visible growth. The control of 25 grains gave an average growth of 19 mm., ranging in length from 3 mm. to 44 mm. Of these 18 made a growth of 10 mm. or more, and the remaining 7 made a growth of less than 10 mm. This shows that when *Zea Mays* is soaked, puncturing the coats does not increase the growth if the opening is blocked by air.* But when unsoaked grains are used and they are in wet sawdust different results are obtained, as is shown by the following experiment.

The average growth of the 24 punctured unsoaked grains was 1.3 mm.; the growth measurements of 7 were as follows, in millimeters: 10, 6, 6, 7, 2, 1, 1, with 17 grains showing no growth. The 24 unpunctured grains gave an average of only 0.3 mm., with 21 having no growth and others ranging in length as follows: 4 mm., 2 mm., and 1 mm. This indicates that when there is no interference from air, moisture is absorbed more regularly and that puncturing of the coat materially increases the growth.

The study of the effect of punctures in different parts of the *Zea Mays* grain was next investigated. In the first experiment the coats were punctured on the opposite side of the grain from the embryo, with the following results. The unsoaked grains were planted in damp sawdust and left for 24 hours. The average growth of 25 grains was 7.04 mm. 2 seedlings were over 40 mm. long, 3 were 15–18 mm. long, 11 were less than 7 mm. long, and 9 showed no growth. The average of 24 unpunctured grains was 3.6 mm., 3 were over 10 mm. long, 7 were less than 10 mm. in length, and 14 showing no growth.

A small puncture was then made in unsoaked grains over the embryo with the fol'owing results: the average growth of 25 grains was 3.24 mm. The length of the growing seedlings was as follows, in millimeters: 25, 19, 14, 10, 7, 3, 2 and 1; while 17 showed no growth. The average growth of 25 unpunctured grains was 1.88 mm. The length of the growing seedlings was as follows, in millimeters: 17, 14, 10, 3, 2, 1; while 19 showed no growth.

The removal of part of the coats from different parts of the grain was made with the following results:

* See de Vries, H. Über künstliche Beschleunigung der Wasseraufnahme in Samen durch Druck. Biol. Centralbl. 35: 161–176. 1915.

1. The seed coat was removed from the large end of the unsoaked *Zea Mays* grain which resulted as follows after 60 hours growth. The average growth of 25 grains was 12 mm. The lengths of the seedlings in millimeters was as follows, 63, 57, 27, 27, 19, 18, 15, 13, 11, 9, 7, 4, 3, 3, 2, 2, 1; while 8 showed no growth. The average growth of 25 seedlings with coats intact was 4.6 mm. The length of these seedlings was as follows, also in millimeters: 36, 26, 20, 10, 9, 8, 2, 3, 1, 1, 1; while 14 showed no growth.

2. The coats were removed from the embryo side of the unsoaked grain and the grain left in the sawdust for 43 hours. The average length of growth of 25 grains was 1.4 mm. The lengths of the seedlings was as follows in millimeters: 17, 12, 4, 3, 2, 1, 1, 1; while 17 showed no growth. The average of 25 grains with intact coats was 0.04 mm., since the only grain germinating made a growth of 1 mm.

3. The coats were removed from one side of *Zea Mays* grains and after 48 hours they showed the following growth. The average growth of 22 grains was 1.9 mm.; the lengths attained by the seedlings were as follows in millimeters: 12, 8, 7, 4, 2, 2, 2, 2, 1, 1, 1, 1; while 10 had no growth. The grains from which the coats had not been partially removed did not make growth enough to break through the coats. These experiments show the decided advantage a grain of *Zea Mays* has when parts of the coats are removed and show that the absorption of water by the endosperm takes place under such circumstances much more rapidly. In this connection it is interesting to consult the paper of A. J. Ewart and Jean White on "The Longevity of Seeds."*

II. EFFECT OF AËRATION ON THE GROWTH OF ZEA MAYS†

This experiment was conducted for the purpose of ascertaining the effect of aëration on the growth of *Zea Mays.* In water cultures, as commonly conducted, the factor of aëration is one that is generally neglected. The plants were grown in most cases as water cultures according to the formula as given by J. Sachs. The cylinders used had a capacity of 1.5 liters and the solution was changed at frequent intervals. The aëration apparatus used in one set of experiments was that of Kekulé, as described by Ostwald.‡ The other piece of apparatus used for aëration was the Bunsen filter pump.

Sachs was the first to experiment with an aëration apparatus on water cultures. This apparatus he illustrates on page 268 and describes on page 269 of his Vorlesungen über Pflanzenphysiologie. The apparatus of Sachs is simple but requires more or less attention, while either of the pieces of the apparatus used for aëration of the cultures mentioned in this paper can be regulated and left for long periods of time to run safely and regularly

* Proc. Roy. Soc. Victoria 21: 1–203. 1908.

† See Beals, C. C. The effect of aeration on the roots of *Zea Mays*—I. Proc. Indiana Acad. Sci. 1917: 177–180. *f. 1–3.* 1918.

‡ Manual of physico-chemical measurements 189. 1894.

without further attention. The Kekulé apparatus as described by Ostwald is very convenient for aëration. The glass tube extends to near the bottom of the cylinder to aërate the solution as perfectly as possible. The resistance can be varied by raising and lowering the tube in the cylinder, and the opening of the tube is slightly contracted to form smaller air bubbles. Care, however, must be used or the resistance will be so great that the water pressure will not force the air bubbles through with sufficient rapidity.

The Bunsen filter pump affords a greater quantity of air than the Kekulé apparatus. From the Bunsen filter pump apparatus numerous lateral tubes can be attached to a main air pipe leading from the pump so that fifteen to twenty cultures can be aërated at once. The supply of air to the individual water cultures is regulated by pinch cocks on the connecting rubber tubes and by raising or lowering these in the solutions.

A short paper appeared by Free* on the aëration of buckwheat, in 1917, in which it was found "that the degree of aeration of the culture solution is without important influence." Stiles and Jörgensen† obtained the same result with buckwheat as Free.

As the columns of air carried down the tube are much larger and of much greater volume than the drops of water, it was found upon measurement that 3.5 times as much air was passed through the solution by the Kekulé apparatus as the volume of water required to convey the air. About 100 c.c. of air were passed through the solution per minute.

TABLE VI

Number of days	Aërated	Non-aërated
2	2.8 c.c.	1.9 c.c.
3	5.9 "	4.7 "
6	14.5 "	12.0 "
8	25.0 "	23.0 "
11	28.0 "	24.0 "
15	37.0 "	33.0 "
20	47.0 "	37.0 "
26	65.0 "	46.0 "

* The effect of aeration on the growth of buckwheat in water-cultures. Johns Hopkins Univ. Circ. 293: 198, 199. 1917.

† Observations on the influence of aeration of the nutrient solution in water culture experiments, with some remarks on the water culture method. New Phytol. 16: 181–197. 1917.

TABLE VI gives the height of the plants at different stages of growth where 100 c.c. of air per minute is used.

After three months' growth under as nearly normal growing conditions as possible, the plants were removed and the amount of ash ascertained. The ash of the aërated plant including the roots were 2.181 grams while the ash of the non-aërated plant weighed 1.303 grams. In another experiment after two months' growth

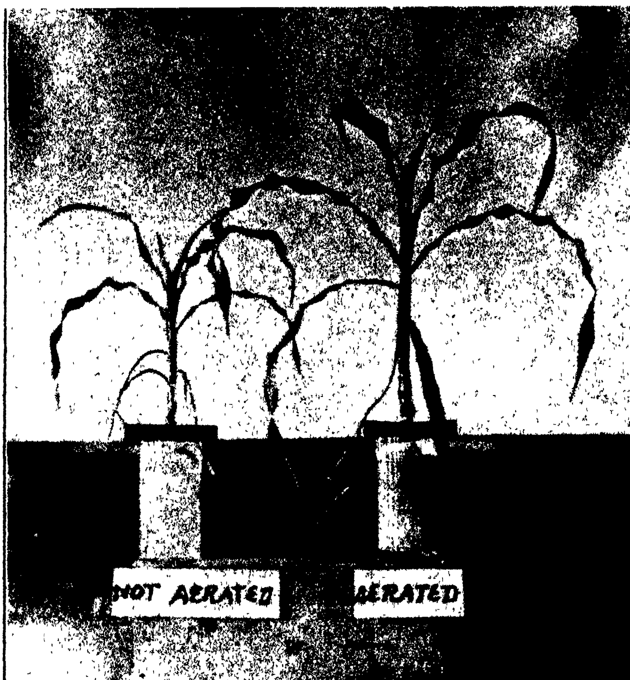


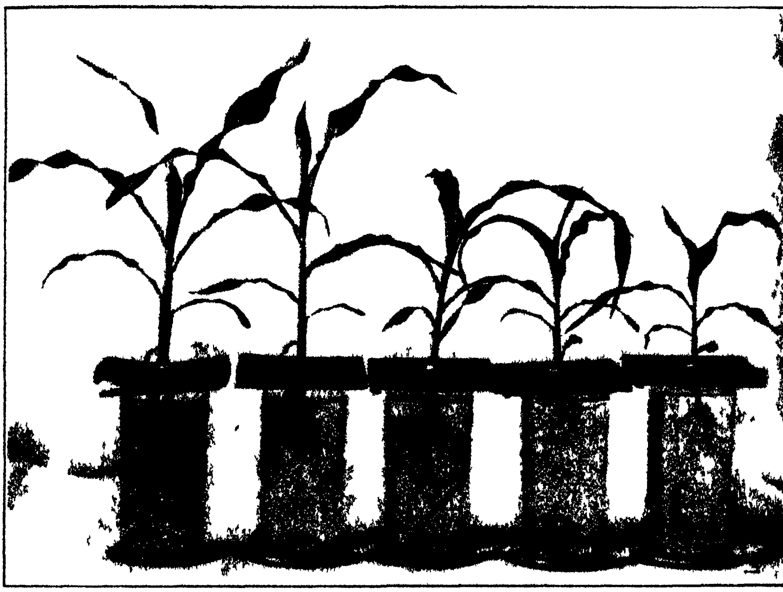
FIG. 1. Non-aërated and aërated specimens of *Zea Mays*.

the ash of the aërated plant (including the roots) weighed 1.855 grams, while the non-aërated plant weighed 0.65 grams or almost three to one in favor of the aëration. The difference is well shown in FIG. 1. The same experiment was performed a number of times, the aërated plant always showing the same marked improvement over the non-aërated one.

Another experiment, shown by FIG. 2, was performed using five cylinders. The air was driven through these cultures by means of a Bunsen Pump apparatus. The culture *A* received

1 liter of air; *B*, 3 liters; *C*, 92 liters, *D*, 120 liters; and *E* 144 liters in 24 hours. The figure shows that the plants made better growth when an increased amount of air was used

The temperature of the culture solution was often too high for good growth. FIG. 3, *A*, is a culture grown without aerating or having the temperature lowered to a favorable point. *B* is a culture which was aerated with about 48 liters of air in 24 hours, but whose culture solution was above a favorable temperature *C* is a



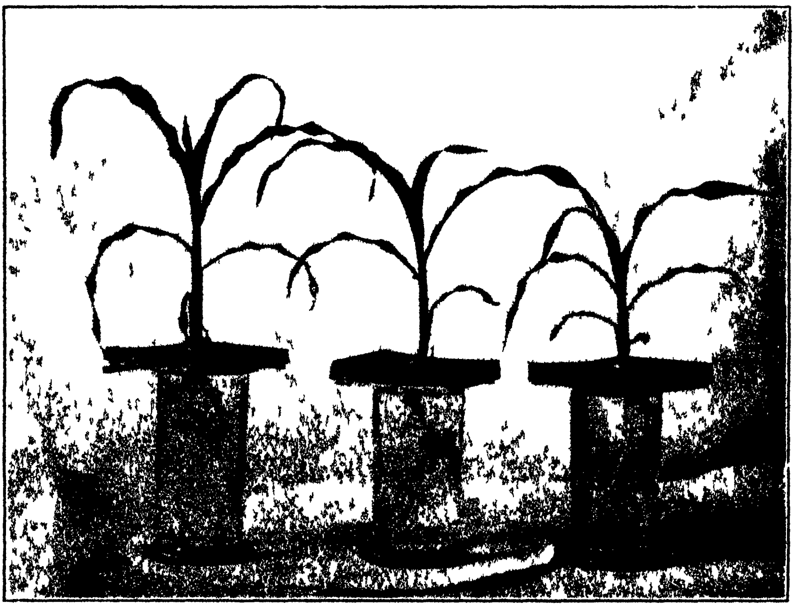
E D C B A

FIG. 2 Effects produced by different quantities of air passed through the culture solution Reading from right to left A received 1 liter in 24 hours, *B*, 3 liters, *C*, 92 liters, *D*, 120 liters, and *E* 144 liters

culture which was aerated with about 48 liters of air in 24 hours and which in addition had the temperature of the culture solution lowered to a favorable point. The temperature in the culture solution of *C* was controlled by placing the glass cylinder containing the roots in a large vessel and allowing a sufficient quantity of water of the desired temperature to flow around it. It is at once seen from the photograph, FIG. 3, that *B* has grown much better than *A*, and that *C* is much larger and has grown faster than *B*. All the cultures were started at the same time and all

the other conditions, except those of areation and temperature, were always the same.

FIGS 4 and 5 show parts of cross-sections of the roots of *Zea Mays* grown in water cultures. FIG 4 is part of a cross-section of a root which had been aerated, and FIG. 5 is the same of a non-aerated root. It will be noticed that the intercellular spaces in the non-aerated root are appreciably larger.



C B A

FIG 3 Effects of temperature and aëration Reading from right to left. *A* was not aerated and was exposed to too high a temperature, *B* was aërated with about 48 liters of air in 24 hours, but was exposed to too high a temperature, *C* was aerated with about 48 liters of air in 24 hours and was exposed to a lower and more favorable temperature

Specimens of *Zea Mays* sometimes suffer for lack of aeration under supposedly normal conditions in the soil. To show this point the following experiment was performed. A large bottle was cut off near the bottom, a perforated rubber stopper was inserted in the neck and a glass tube put through this for the admission of air. The bottle was inverted, about 1 cm. in depth of melted paraffin poured over the cork to exclude the air and the lower part filled with wet sphagnum and this covered over with

moist earth to a depth of about two decimeters. A young *Zea Mays* plant was placed in the soil and melted paraffine was poured over the surface after placing a small short paper cylinder around the plant. The paraffine caused all the air from the aërating apparatus to come out around the plant and not escape around the sides of the bottle or elsewhere before coming in contact with the roots. The bottle was supported on a ring-stand and the small glass tube attached to the aërating apparatus. The apparatus offered practically no resistance to the air supply as was shown by a

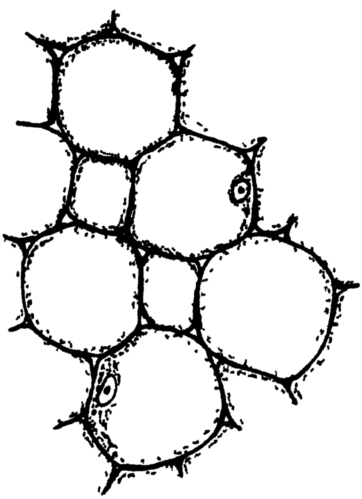


FIG. 4.

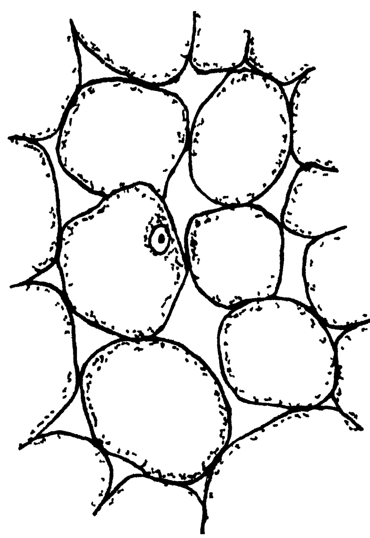


FIG. 5.

FIG 4. Part of a cross section of a root of *Zea Mays* grown in an aerated water culture. FIG. 5. Part of a similar section of a root from a non-aerated water culture.

manometer. A control plant was planted in a pot and set on the bench near by. The aërated plant in this case made almost as great a gain over the non-aërated as the ones so treated in the water cultures, showing that the increase was due to the presence of a greater amount of air. All the other conditions except that of aëration were the same for both specimens in this experiment.

SUMMARY

1. The best length of time for soaking the grains of *Zea Mays* used in these experiments was 12 hours.

2. Puncturing the coats of the grains or the removal of a portion of the coats accelerates, as would be expected, the germination under proper conditions.

3. Too long soaking materially retards the growth for a time.

4. Aërating the culture solution accelerates the growth.

INDIANA UNIVERSITY

INDEX TO AMERICAN BOTANICAL LITERATURE

1918–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Vol. 46 No. 4

BULLETIN

OF THE

TORREY BOTANICAL CLUB

APRIL, 1919

New species of Uredineae—XI *

JOSEPH CHARLES ARTHUR

The preceding number in this series† was issued in April, 1918. Studies since that time have shown that two species given there were founded upon a misinterpretation of the hosts. The material submitted by the collector for *Puccinia wyomensis* (Bull. Torrey Club **45**: 143) consisted of three culms of *Scirpus americanus*, two of them fertile. These were about a foot long, once folded, and were intermixed with two fragments of culms and about twenty pieces of leaves averaging six inches long, having a similar appearance. Not until after publication was it ascertained that the material was separable into culms of *Scirpus* and leaves of what is undoubtedly an *Agropyron*. The rust is wholly on the *Agropyron*, although the *Scirpus* is discolored and wrinkled in a way to simulate the grass leaves. The rust proves to be *Puccinia Clematidis* (DC.) Lagerh., of which *P. wyomensis* thus becomes a synonym. Recently the collector has distributed (Barth. N. Am. Ured. *1999*) what purports to be the type collection of this form, but which wholly consists, so far as the specimen coming to the writer shows, of *Puccinia obtecta* Peck, on *Scirpus americanus*.

* Reprints may be obtained by application to the Botanical Department, Purdue University Agricultural Experiment Station, Lafayette, Indiana, under whose auspices the studies here reported were largely carried out.

† New species of Uredineae I–X: Bull. Torrey Club (I) **28**: 661–666. 1901; (II) **29**: 227–231. 1902; (III) **32**: 1–8. 1904; (IV) **33**: 27–32. 1906; (V) **33**: 513–522. 1906; (VI) **34**: 583–592. 1907; (VII) **37**: 569–580. 1910; (VIII) **38**: 369–378. 1911; (IX) **42**: 585–593. 1915; (X) **45**: 141–156. 1918.

[The BULLETIN for March (**46**: 73–106, *pl. 6, 7*) was issued March 10, 1919.]

A somewhat similar error occurs in connection with *Puccinia missouriensis* (*l. c.* p. 146). In making studies for the genus *Allodus*, Professor C. R. Orton made the discovery that the host, consisting of a small fragment, 2 by 3–5 cm., is not *Ranunculus recurvatus* as stated by the collector, but is in reality *Anemone cylindrica* A. Gray, and that the telia on it belong to *Puccinia Anemones-virginianae* Schw., while the aecia belong to *P. Clematidis* (DC.) Lagerh.

A number of grass rusts, now known only in their uredinial form, undoubtedly belong either to the genus *Puccinia* or *Uromyces*. For the sake of convenience in listing such species it is proposed to transfer two of these names without waiting for the discovery of the telial form. They will be placed under *Puccinia*, as the chances are two out of three that they will eventually be found to belong in that genus rather than in *Uromyces*. In the case of three other species of grass rusts long known under the genus *Uredo* the teliospores have recently been discovered and, in the case of two of them, on type material, entitling them to a place under *Puccinia*.

The wholly new species here proposed, some sixteen in all, are partly taken from recent collections, but more largely from material which has been long in the herbarium awaiting study. While a few of these came from the northern states, they are largely from the southern border of the United States, from Mexico and the West Indies. I have been given the privilege to include species derived from the studies of Professors Jackson, Holway and Bethel, which with others here published are shortly to be made part of the seventh volume of the North American Flora.

Puccinia egressa nom. nov.

Puccinia egregia Arth. Bull. Torrey Club **38**: 370. 1911. Not *P. egregia* Arth. 1905.

Through pure inadvertance the same specific name has been given by the writer to two unrelated rusts. The first opportunity since noticing the mishap is now taken to replace the later one, the species being on *Baccharis oaxacana* Greenm., still only known from the type collection made on Mt. Oaxaca, Mexico, by C. G. Pringle, in 1894.

Puccinia (?) **fuirenicola** nom. nov.

Uredo Fuirenae P. Henn. Hedwigia **38**: Beibl. [70.] 1899. Not *Puccinia Fuirenae* Cooke, 1878.

The type of this species was collected at St. Catherine near San Francisco, Brazil, in 1884, by E. Ule, No. 15. It is on *Fuirena umbellata*, the same species of host on which it occurs in Cuba, Porto Rico, and India. The author of the species so named it because he thought it probably a form of *Puccinia Fuirenae* Cooke, whose uredinia had not then been described. The urediniospores differ decidedly, however, from those of that species in size, thickness of wall, and number of pores. Teliospores are not known.

Puccinia (?) **Scribnerianum** nom. nov.

Uromyces Aristidae Ellis & Ev. Jour. Myc. 3: 56. 1887. Not *U. Aristidae* of later authors, or *Puccinia Aristidae* Tracy.

Only the type collection of this species is known. It shows prominent sori with large, thick-walled urediniospores and strongly developed paraphyses. The type specimen in the Ellis Herbarium at the New York Botanical Garden is labelled "*Uromyces Aristidae* Ellis & Ev. on leaves of *Aristida Arizonica* Vasey, New Mexico." Within the packet is a note indicating that the material was communicated by Prof. Scribner: "The Uromyces Aristidae I found on the lvs. of an herbarium specimen of the Aristida from New Mexico. I send you half of the material I found. F. L. Scribner." A fragment of the same collection is in the Farlow Herbarium at Harvard University, communicated by J. B. Ellis, which gives the locality as "Arizona" instead of New Mexico. Parts of these two specimens were transmitted to Professor A. S. Hitchcock at Washington, D. C., with the request that he look over the grass herbarium to see if the host could be matched or verified. He replied under date of November 3, 1913: "I have looked over the specimens of *Aristida arizonica* [in the National Herbarium], and I find one collected in New Mexico in 1884 upon which there is a rust apparently the same, so far as external appearances go, as the one on your specimens. This sheet [No. 745514] was formerly a part of the Scribner Herbarium, recently acquired by the National Herbarium. It is true that your specimen is said to have come from Arizona, and the published locality of the

[phanerogamic] specimen is Arizona, yet all the specimens in our herbarium upon which Dr. Vasey left a record, many of them with numerous notes and descriptions, are from New Mexico, and what I regard as the type of the species in spite of the published locality is from New Mexico." Professor Hitchcock kindly sent a portion of the rusted leaves from the phanerogamic specimen, which proved to be identical in microscopic characters with the Ellis specimen. It is clearly evident that only one collection of the rust is known, partly in the Ellis collection in New York, partly in the Farlow Herbarium at Cambridge, and partly in the National Herbarium at Washington, which was collected by Dr. George Vasey at Santa Fe, New Mexico, in 1884, and communicated to Mr. Ellis by F. L. Scribner. The dark color of the spores must have led Mr. Ellis to call it *Uromyces*, thinking he had telia rather than uredinia. No trace of teliospores has yet been discovered.

The species of *Uromyces*, which had been commonly called *U. Aristidae*, having urediniospores unlike those of the present species, and with teliospores usually present, was named *U. seditiosus* by Dr. F. D. Kern (Torreya **11**: 212. 1911), who pointed out the peculiar situation regarding the Ellis material. Again it seems desirable to explain the chain of circumstances making it necessary to give a new name to this imperfectly but long recognized rust. Although the teliospores are not known it will be placed under the genus *Puccinia* for convenience in listing.

Puccinia Kaernbachii (P. Henn.) comb. nov.

Uredo Kaernbachii P. Henn. Bot. Jahrb. **18**: Beibl. [22]. 1894.

II. Uredinia hypophyllous, numerous, in lines, often confluent, elliptic, 0.5–1.3 mm. in length, long covered by epidermis, chestnut-brown; paraphyses peripheral, usually erect, clavate-capitate, 15–18 by 32–55 μ, the wall pale cinnamon-brown, 2–2.5 μ thick, thicker above, 7–10 μ; urediniospores broadly ellipsoid or obovoid, 18–24 by 26–32 μ; wall chestnut-brown, 1.5–2 μ thick, uniformly, finely and closely echinulate, the pores usually 4, equatorial.

III. Telia similar to uredinia; teliospores oblong or oblong-ellipsoid, 16–19 by 35–48 μ, usually rounded above and below, moderately constricted at septum; wall chestnut-brown, 1–2 μ thick, thicker above, 5–7 μ, smooth; pedicel concolorous, fragile.

On *Andropogon stolonifer* (Nash) Hitchc., Brevard County, Florida, October 16, 1903, *A. Fredholm 6122;* Hillsborough

County, Florida, September 27, 1904, *A. Fredholm 6406*. Both collections were communicated in the spring of 1917 by Mrs. Agnes Chase, who separated them from specimens in the grass herbarium of the U. S. National Herbarium.

Andropogon stolonifer is closely related to *A. scoparius* Michx., differentiated from it chiefly by having well-developed stolons. The two belong to the genus section *Schizachyrium*, while *A. Schoenanthus* L., the host of Hennings' *Uredo Kaernbachii*, belongs to the section *Cymbopogon*. It is the opinion of Mrs. Chase that the plant intended by "*A. Schoenanthus*" may be one of the oil grasses that passed under that name. However, Stapf has shown that the true *A. Schoenanthus* is the desert grass called *A. laniger* Desv.

Puccinia pallescens nom. nov.

Uredo pallida Diet. & Holw.; Holway, Bot. Gaz. **24**: 37. 1897. Not *Puccinia pallida* Tracy, 1893.

II. Uredinia amphigenous, oval or oblong, pale yellowish; paraphyses none; urediniospores ellipsoid, obovoid or pyriform, 13–21 by 20–29 μ; wall colorless or nearly so, thin, about 1 μ, finely and moderately echinulate, the pores equatorial, very indistinct, probably 4.

III. Telia hypophyllous, scattered or associated in rather indefinite groups about 1 cm. across, oval or oblong 0.5–2 mm. long, covered by the epidermis, very compact and stromatoid, brownish-black due partly to discoloring of surrounding host tissue; teliospores cylindric, 1–4-celled, usually 2- or 3-celled, 9–16 by 26–67 μ, truncate or rounded at both ends, slightly or not constricted at septum; wall light golden-brown, thin, 1 μ, slightly thicker above, 2–3 μ, smooth; pedicel very short or lacking.

On *Tripsacum lanceolatum* Rupr., near City of Mexico, Mexico, October 1, 1896, II, *Holway* (type of *Uredo pallida*); Tizapan, near City of Mexico, Mexico, September 27, 1899, II, *Holway 3504*.

On *Tripsacum latifolium* Hitchc., Aguacalientes, Dept. Santa Rosa, Guatemala, January 25, 1908, II, iii, *Kellerman 7802;* Jinotepe, Nicaragua, November 3–7, 1911, II, III, *Hitchcock* (phan.) *8720;* Volcano of San Salvador, Salvador, November 20–26, 1911, II, *Hitchcock* (phan.) *8947*.

On *Zea Mays* L., Naguabo, slope of El Duque, Porto Rico, April 19, 1916, II, *Whetzel & Olive 440*.

The telia of this species have recently been detected by Dr. E. B. Mains and prove to be even more distinctive than the uredinia. They occur in abundance on the Nicaraguan collection and sparingly on the one from Guatemala, both specimens having been communicated by Mrs. Agnes Chase, who found them in the grass collection of the Department of Agriculture. The telia elevate the epidermis slightly, but are readily found on account of the brown coloration of the surrounding cells. They look, however, more like some species of *Phyllachora* than a *Puccinia*. The teliospores themselves are pale brown and translucent. Owing to the firmness of the enveloping tissues and the delicacy of the teliospores a scraped mount usually shows only the upper part of the teliospores, resembling a parenchymatous mass of tissue. Sections are required to reveal the form of the teliospores; they show that the central spores of the sorus are usually three-celled, while the peripheral spores are often one-celled. Generally the two-celled teliospores predominate.

The type collection and the later one from the same region were first reported as on *Tripsacum dactyloides*, but were later found to be on *T. lanceolatum*. Both collections show the characteristic small, pale urediniospores, but they also show much larger, thick-walled urediniospores of another rust, and in the case of one of them a few teliospores also. This association on the same leaves led at one time (Bull. Lab. Hist. Univ. Iowa 5: 174. 1901) to the assumption that only one species was involved (*P. Tripsaci* Diet. & Holw., now referred to *P. Ceanothi* [E. & K.] Arth.), the larger urediniospores being called amphispores.

The urediniospores on *Zea Mays* are somewhat larger than those on *Tripsacum*. But as those on the collection of *Paspalum* from Guatemala, having two-inch-wide leaves resembling those of maize, are intermediate in size, and as no other grass rust is known having such urediniospores, the collection is assumed to belong here, awaiting the discovery of telia on this host. The size of the urediniospores apparently bears a direct relation to the succulency of the host.

Puccinia imposita nom. nov.

Uredo Muhlenbergiae Diet.; Atkinson, Bull. Cornell Univ. 3: 22. 1897. Not *Puccinia Muhlenbergiae* Arth. & Holw. 1902.

II. Uredinia amphigenous on brownish or purplish spots, early or somewhat tardily naked, cinnamon-brown; urediniospores globoid or broadly ellipsoid, 23–32 by 27–35 µ; wall cinnamon-brown, rather thick, 1.5–2.5 µ, closely and finely echinulate, the pores prominent, equatorial, 3 or 4, covered with swollen, hyaline cuticle.

III. Telia disposed similarly to the uredinia, chestnut-brown; teliospores oblong or clavate, 18–26 by 37–48 µ, rounded at both ends or slightly narrowed below, usually not constricted at septum; wall dark chestnut-brown above, lighter below, 1.5–2.5 µ thick, thickened 6–8 µ at apex, sometimes also thickened at one side; pedicel golden-brown, short.

On *Leptoloma cognatum* (Schultes) Chase (*Panicum cognatum* Schultes), Auburn, Lee County, Alabama, August 31, 1890, II, iii, *Geo. F. Atkinson 1586* (type); Ellsworth County, Kansas, July 27, 1896, II, iii, *C. H. Thompson;* Austin, Texas, February 27, 1901, II, *W. H. Long, Jr. 82;* Austin, Texas, November 10, 1914, II, *Lewis & Tharp 41;* Stillwater, Oklahoma, July 27, 1915, II, *C. D. Learn 128;* Austin, Texas, October 29, 1915, II, III, *B. C. Tharp.* The type collection had the host given as probably *Muhlenbergia diffusa.* The material is scanty and without inflorescence. Its identity was ascertained through the painstaking examination made by Mrs. Agnes Chase. On July 16, 1915, she wrote; "The specimen marked '*Muhlenbergia diffusa*' I make *Leptoloma cognatum.* They have the same texture and ligule, and the little erect bit of firm tissue on either side at the summit of the sheath, where in aged leaves it tears loose from the thin ligule as found in *Leptoloma.*" The teliospores were discovered on type material in April, 1911, but it was not until the host was positively identified that the relationship of the rust could be worked out.

Puccinia Cockerelliana Bethel, sp. nov.

O. Pycnia amphigenous, few, 107–128 µ broad.

I. Aecia hypophyllous or caulicolous, in small groups 3 mm. or less across, low cupulate; peridium soon disappearing; peridial cells rhombic, 16-23 by 27–35 µ, the outer wall thick, 6–8 µ, smooth, the inner wall thinner, 2–3 µ, coarsely verrucose; aeciospores angularly globoid, 18–24 by 20–29 µ; wall nearly or quite colorless, moderately thick, 1.5–2.5 µ, finely and evenly verrucose.

II. Uredinia epiphyllous, intercostal, oblong-linear, 0.5–1

mm. long, cinnamon-brown; urediniospores ellipsoid, 19–26 by 24–32 μ; wall colorless or nearly so, 1.5–2 μ thick, finely echinulate, the pores obscure, probably scattered.

III. Telia similar to the uredinia, long covered by the epidermis, becoming dehiscent by a longitudinal slit, grayish-black; teliospores not surrounded by stromal hyphae, cylindric or clavate-cylindric, 13–21 by 50–85 μ, rounded or truncate above, tapering to base, the upper cell about one third length of spore, slightly or not constricted at septum; wall chestnut-brown above, paler below, thin, about 1 μ, moderately thickened above, 3–7 μ; pedicel short, tinted.

On *Thalictrum Fendleri* Engelm., Gunnison County, Colorado, September 2, 1899, I, *E. Bartholomew;* Eldora, Colorado, 9,000 feet alt., July 25, 1910, I, *E. Bethel* (Barth. N. Am. Ured. *616*); Eldora, Colorado, June 24, and July 2, 1911, I, *E. Bethel;* Trout Lake, 10,000 feet alt., August 2, 1912, I, *F. D. Kern 5107;* Trimble Springs, nine miles from Durango, Colorado, 7,500 feet alt., August 4, 1912, I, *F. D. Kern 5303.*

On *Festuca Thurberi* Vasey, Eldora, Colorado, 9,000 feet alt., September 17, 1910, III; same, May 20, June 24, July 4 (type), October 7, 1911, III; same, June 30, 1912, III; same, September 19, 1914, III; same, July 22, 1916, III, all collected by *E. Bethel;* same, August 25, 1911, II, *Bethel & Kern;* Fremont Station near Manitou, Colorado, August 25, 1916, II, III, *J. M. Bates 6486.*

As early as 1910 Mr. Bethel wrote in transmitting specimens that these forms of rust on *Thalictrum* and *Festuca*, found growing together and apparently genetically connected, were noticeably different from the forms belonging under *Puccinia Clematidis.* He then transplanted healthy plants of both hosts to his garden in Denver, and the following year began a series of cultures, using both aeciospores and teliospores, which has extended to the present time. Some of the results of these numerous trials have been transmitted to the writer; the publication of a full account of the work, however, is contemplated by Mr. Bethel, who has supplied the name and nearly all the information regarding the species, and it is deemed neither necessary nor courteous to give more than a bare statement in this connection. Mr. Bethel also sent telial culture material several times to the writer, from which only one successful germination of spores was obtained. A culture followed, the result being recorded in a report of cultures for 1915 (Mycologia **8**: 132. 1916) under the name *Puccinia Agropyri.*

Puccinia Cockerelliana is conspicuously different in both gross and microscopic appearance from *P. Agropyri*, which occurs on the same and other similar hosts. The aecia are more crowded, more robust and more inclined to be bullate; the aeciopsores are larger and have much thicker walls. The telia are on the rough or morphologically upper side of the leaf and situated between the veins, instead of on the smooth side of the leaf or on sheaths and stems as in *P. Agropyri*. The telia are also larger, and become normally dehiscent and uncovered after a time. The teliospores are very long and slender, and have no enveloping stromal mass, as commonly found in strictly subepidermal forms.

The species is named by Mr. Bethel in recognition of the eminent services rendered science in many fields by Professor T. D. A. Cockerell, of the University of Colorado, Boulder, Colorado, and especially to recall his help in studying the flora of Colorado, including the rusts and other fungi.

Puccinia inclita sp. nov.

II. Uredinia amphigenous, tardily naked, brownish-yellow; urediniospores globoid or ellipsoid, 22–26 by 24–32 μ; wall pale yellow or brownish-yellow, thin, 1–2 μ, coarsely and sparsely echinulate with elongated and sharply pointed projections, the pores obscure, doubtless 3 and approximately equatorial.

III. Telia similar to the uredinia, chocolate-brown; teliospores broadly ellipsoid or oblong, 26–29 by 35–40 μ, rounded at both ends, very slightly or not constricted at septum, often with mesospores intermixed, 23–27 by 26–29 μ; wall chestnut-brown, 2.5–3.5 μ thick in upper cell and somewhat thinner in lower cell, thicker above, 3–6 μ and often slightly lighter in color, smooth; pedicel golden-brown or paler, the diameter uniform, about one and one half times length of spore.

On *Ichnanthus pallens* (Sw.) Munro, Mayagüez, Porto Rico, March 2, 1916, II, *Whetzel & Olive 396*; El Yunque, Porto Rico, April 12, 1916, II, III, *Whetzel & Olive 397* (type).

On *Oplismenus hirtellus* (L.) R. & S., Las Marias, Porto Rico, July 10, 1915, II, *F. L. Stevens 8118*.

The striking appearance of the urediniospores with their prominent echinulation caused the first collection studied, that by Professor Stevens on *Oplismenus*, to be referred to the South American *Uredo Olyrae* P. Henn. (see Mycologia **8**: 21. 1916), but

it was afterward placed under *Uredo paspalicola* P. Henn. (see Mycologia 9: 92. 1917). The other two collections, those by Whetzel & Olive on *Ichnanthus*, were placed under *Puccinia substriata* Ellis & Barth. (see Mycologia 9: 73. 1917), a species now considered to include *Uredo paspalicola*. More intimate and extended comparisons, however, have led to the belief that this form should be separated from the widely distributed and variable *P. substriata*. The most characteristic features are the large and usually pale urediniospores, with their thin walls, sparsely covered with spine-like points. The spores were at first thought to be thick-walled (see Mycologia 8: 22. 1916), an error due, as in many other cases, to mistaking the dense ectoplasm of the cell as part of the wall.

Puccinia Coelopleuri sp. nov.

O. Pycnia amphigenous or petiolicolous, crowded in groups 1–2 mm. in diameter, noticeable, subepidermal, globoid, 96–112 μ in diameter; ostiolar filaments short.

II. Uredinia amphigenous; the primary form sometimes petiolicolous, crowded, circinating about the pycnia in round or oblong groups 2–10 mm. long, oblong, 0.5–4 mm. long, early naked, pulverulent, cinnamon-brown, ruptured epidermis conspicuous, the secondary form scattered over the surface of the leaves unaccompanied by pycnia, oval, 0.2–0.5 mm. long, otherwise like the primary form; urediniospores broadly obovoid or ellipsoid, 22–26 by 27–35 μ; wall cinnamon-brown, 2–2.5 μ thick, much thicker above, 3–7 μ, moderately echinulate, the pores 3, equatorial, covered by the colorless swollen cuticle.

III. Telia mostly hypophyllous, scattered, oval, 0.2–0.5 mm. long, early naked, somewhat pulverulent, chocolate-brown, ruptured epidermis evident; teliospores cylindric, oblong or oblong-clavate, 15–20 by 37–63 μ, rounded at both ends, or slightly narrowed below, not or slightly constricted at septum; wall dark cinnamon-brown, thin, 1–2 μ, slightly thickened at apex, 3–4 μ, smooth; pedicel colorless, fragile, short.

On *Coelopleurum Gmelini* (DC.) Ledeb., Juneau, June 20, 1917, No. *355*, July 18, 1918, No. *481*; Mendenhall, June 24, 1917, No. *366*, September 9, 1917, No. *387* (type), August 3, 1918, No. *487*; Haines, August 21, 1918, No. *501*, all from Alaska, and collected by *J. P. Anderson*. A conspicuous and, on account of its large spores, a striking species.

Puccinia parca sp. nov.

II. Uredinia hypophyllous, scattered or irregularly grouped, roundish, 0.3–0.6 mm. across, brownish-yellow, pulverulent; urediniospores narrowly ellipsoid or obovoid, 13–16 by 19–26 μ; wall brownish- or light-yellow, very thin, 1 μ or less, moderately and inconspicuously echinulate, the pores indistinct, 2–4, equatorial or superequatorial.

III. Telia similar but slightly larger than the uredinia, dark cinnamon-brown, pulverulent; teliospores ellipsoid or oblong, 15–19 by 29–42 μ; wall cinnamon-brown, rather thin, 1–2 μ, thickened into a hemispherical hyaline papilla over the pores, 4–5 μ, smooth; pedicel colorless, one half length of spore or less, fragile.

On *Tiniaria scandens* (L.) Small (*Polygonum scandens* L.), Flatbush, Long Island, New York, October 5, 1889, II, III, *J. L. Zabriskie 703;* Stelton, New Jersey, September 7, 1892, II, III, *Byron D. Halsted* (Seym. & Earle, Econ. Fungi *367*, type); Laurel Springs, northwestern North Carolina, September 20, 1904, II, III, *H. H. Hume 278*. As long ago as October, 1905, Professor Holway called the attention of the writer to the peculiarities of the rust issued by Seymour & Earle in their Economic Fungi under the name of *P. mammillata*. Professor Holway pointed out that that species has rough spores and of a different shape from this material. He thought it might be a new species, but later in his North American Uredineae (**1**: 40) placed it doubtfully under *P. septentrionalis* Juel. *P. septentrionalis* is a boreal species on *Bistorta viviparum*, having its aecia on *Thalictrum alpinum*, and in America has been taken in Alaska and Newfoundland. The rust in question agrees with *P. septentrionalis* in the character of its teliospores, as Professor Holway pointed out in detail, but differs from it in having slightly narrower urediniospores, with thinner walls, of a lighter and more yellowish color. The species is markedly distinct from *P. Polygoni* A. & S., the common rust on the same and related hosts, both in the teliospores and urediniospores. The pores of the urediniospores are difficult to make out, but are usually three and approximately equatorial, while in the more common *P. Polygoni* they are distinct and two in the upper part of the spore.

Puccinia gentilis sp. nov.

II. Uredinia hypophyllous, scattered, round or elliptic, 0.3–0.8 mm. across, pulverulent, cinnamon-brown; urediniospores oblate-spheroid, 23–26 μ broad by 19–24 μ long, or globoid to obovoid, 21–23 by 21–28 μ; wall dark cinnamon-brown, 1.5–2 μ thick, moderately and strongly echinulate, the pores 2 or 3, subequatorial or approximately equatorial.

III. Telia hypophyllous, similar to the uredinia, becoming pulverulent, blackish-brown; teliospores broadly ellipsoid, 27–32 by 35–45 μ, rounded above and below, not constricted at septum; wall chocolate-brown, thick, 3–5 μ, thickened over the germ-pore into a yellowish umbo, 7–10 μ thick, moderately verrucose with markings uniting into short irregular lines giving a coarsely verrucose appearance; pedicel colorless, with thin walls, 1 μ or less, twice length of spore.

On *Salvia alamosana* Rose, Oaxaca, Mexico, October 21, 1899, II, iii, *E. W. D. Holway 3699; Salvia* sp., Oaxaca, Mexico, October 18, 1899, II, III, *E. W. D. Holway 3666* (type). The species is in many respects similar to *Puccinia mitrata* Syd., but the urediniospores are larger and more prominently echinulate.

Puccinia prospera sp. nov.

II. Uredinia amphigenous, scattered, round, 0.2–0.8 mm. in diameter, pulverulent, cinnamon-brown; urediniospores oblate spheroid, 25–30 μ broad by 20–23 μ long; wall cinnamon-brown, 1.5 μ thick, moderately and rather strongly echinulate, the pores 2 or 3, subequatorial.

III. Telia hypophyllous, similar to the uredinia, pulverulent, chestnut-brown; teliospores broadly ellipsoid, 27–32 by 35–40 μ, rounded above and below, not constricted at septum; wall chestnut-brown, rather thin, 1–2.5 μ, thickened over the germ-pores, 5–7 μ, obscurely verrucose-rugose; pedicel colorless, fragile, once to once and half length of spore, thin-walled, fragile.

On *Salvia microphylla* H. B. K., Toluca, Mexico, September 17, 1898, II, *E. W. D. Holway 3136;* Pachuca, Mexico, October 5, 1899, II, III, *E. W. D. Holway 3579* (type). Another species of the *P. mitrata* group, the teliospores being of the same size as those of that species, but with the thickness of wall and its markings like *P. farinacea* Long. The urediniospores also have the size of *P. farinacea.*

Puccinia massalis sp. nov.

O. Pycnia amphigenous and caulicolous, rather conspicuous, subepidermal, 112–120 μ broad.

I. Aecia amphigenous and caulicolous, crowded in irregular groups 2–10 mm. across on the blades, often 6–20 mm. long on the stems, petioles and veins, causing distortion of the host, cylindric, 0.5–0.8 mm. in diameter, 0.5–1 mm. high; peridium with erect margin, erose or somewhat lacerate; peridial cells rhombic, 19–27 by 32–45 μ, the outer wall 7–10 μ thick, smooth, the inner wall 5–10 μ, closely tuberculate; aeciospores ellipsoid, 16–18 by 22–27 μ; wall colorless, 1.5–2 μ thick, very closely and inconspicuously verrucose.

II. Uredinia amphigenous, scattered, round, 0.8–1.2 mm. in diameter, pulverulent, cinnamon-brown; urediniospores irregularly ellipsoid, obovate or oblong, 18–24 by 27–35 μ; wall light cinnamon-brown, 1–1.5 μ thick, moderately echinulate, the pores 2, equatorial.

III. Telia similar to the uredinia, pulvinate, chocolate-brown; teliospores ellipsoid, 23–32 by 39–48 μ, rounded above and below, slightly or not constricted at septum; wall dark chestnut-brown, thick, 3–5 μ, thickened and lighter-colored over the germ-pores, 9–10 μ, smooth, the pore of upper cell apical, of lower cell usually half way to hilum or occasionally at septum; pedicel colorless, once to thrice length of spore.

On *Helianthus ciliaris* DC., Las Cruces, New Mexico, October 27, 1892, I, III, *E. O. Wooton;* Ysleta, Texas, February 24, 1914, III, *Arthur & Fromme 5704;* Mesilla Park, New Mexico, October 7, 1914, III, and May 9, 1915, I, *W. A. Archer;* Albuquerque, New Mexico, December, 1914, III, *W. H. Long 5183;* Brazito, New Mexico, June 15, 1915, I, II, III, *W. A. Archer* (type). This is a much more robust species than *Puccinia Helianthi* Schw., to which most of the collections here cited have been referred (Mycologia **8**: 159. 1916). The aecia are much larger, and cause swelling of the adjacent tissues, even giving the appearance in some cases of being a systemic rust. Both the aeciospores and teliospores have far thicker walls.

Puccinia invelata Jackson, sp. nov.

O. Pycnia epiphyllous, gregarious, few, inconspicuous, subepidermal, 115 μ broad.

I. Aecia hypophyllous, solitary or in groups of two or three; peridium lacerate; peridial cells ellipsoid, 14–18 by 27–35 μ, over-

lapping, the wall 3 μ thick; aeciospores ellipsoid, 16–23 by 24–26 μ; wall 1–1.5 μ thick, closely verrucose.

II. Uredinia hypophyllous, scattered, roundish, small, 0.2–0.4 mm. across, moderately pulverulent, cinnamon-brown; urediniospores globoid, ellipsoid or obovoid, 20–26 by 24–29 μ; wall cinnamon-brown, 1.5–2 μ thick, prominently echinulate, the pores 2, surrounded by an indistinct smooth area, equatorial.

III. Telia hypophyllous or somewhat amphigenous, scattered, roundish, small, 0.1–0.4 mm. across, early naked, compact, chestnut-brown; teliospores ellipsoid or obovate, often somewhat irregular, 19–26 by 32–45 μ, obtuse or rounded above, more or less narrowed below, slightly constricted at septum; wall cinnamon-brown, laminate, thin, 1.5–2.5 μ thick, much thicker above, 7–10 μ, with distinct and somewhat paler umbo; pedicel colorless, once to once and a half length of spore, usually breaking away.

On *Verbesina montanoifolia* Robs. & Greenm., Patzcuaro, Mexico, October 16, 1898, ii, III, *3000* (Barth. Fungi Columb. *5055*); Morelia, Mexico, October 8, 1899, ii, III, *3592* (Barth. N. Am. Ured. *426*); Patzcuaro, Mexico, October 10, 1899, O, I, II, III, *3606–7* (type), all collections by *E. W. D. Holway*. The species differs from *P. abrupta* Diet. & Holw., which occurs on the same and other species of *Verbesina*, by the strongly obovate teliospores with somewhat narrowed base, paler and thinner walls, and more fragile pedicel. The *Verbesina* rusts have recently been studied by Professor H. S. Jackson, who has separated this form as a new species and supplied the name and diagnosis.

Uromyces Shearianus nom. nov.

Aecidium Atriplicis Shear, Bull. Torrey Club **29**: 453. 1902.
Uromyces Atriplicis Arth. Bull. Torrey Club **45**: 141. 1918.
Not *U. Atriplicis* McAlpine, 1906.

In the preceding number of this series the writer transferred the early specific name of this rust to another genus without noticing that it had already been used in that connection for a wholly unlike rust occurring in Australia. Although regretting the unnecessary synonym I am pleased to have the opportunity to dedicate the species to Dr. C. L. Shear, who first described it, and who has done notable service in many ways in the field of mycology.

Uredo biporula sp. nov.

II. Uredinia hypophyllous, chiefly scattered or somewhat gregarious, orbicular, 0.2–0.3 mm. in diameter, soon naked, pulverulent, dark cinnamon-brown; urediniospores triangular-obovoid, 21–23 by 23–26 μ; wall dark cinnamon-brown, 1-2 μ thick, moderately and finely echinulate, the pores 2, basal, and close to the hilum.

On *Salvia fulgens* Cav., Amecameca, Mexico, October 31, 1899, *E. W. D. Holway 3758*. This collection, in which the uredinia are abundant and conspicuous, shows the unique character among *Salvia* rusts of two basal pores in the urediniospores.

Uredo amicosa sp. nov.

II. Uredinia hypophyllous, scattered, bullate, 0.2–0.4 mm. in diameter, opening by a central pore; paraphyses thickly imbricated, the united bases forming a tissue-like lining to the sides of the sorus, the long free ends cylindric or fusiform-cyclindric, 10–16 by 67–112 μ, acuminate or acute, the wall colorless, thickened to nearly or quite obliterate the lumen; urediniospores epedicillate, angularly oblong, ellipsoid, or obovoid, 23–34 by 40-60 μ; wall golden-brown, 2-3 μ thick, sometimes twice as thick at apex, sparsely and strongly echinulate, the pores obscure, possibly 3 or 4 and equatorial.

On *Chrysophyllum Cainito* L., mesas near Mayagüez, Porto Rico, March 29, 1917, *H. E. Thomas 264*. There are many sapotaceous rusts, but this one on the common star apple of the tropics seems to be different from any heretofore described. The rather conspicuous sori are abundantly scattered over the under side of the leathery leaves. The spores may possibly be catenulate, as no pedicels can be detected, either attached to the spores or at the bottoms of the sori. Two species of *Uredo* have been described on undetermined species of *Chrysophyllum* from Brazil, but both of them have much smaller spores and quite different sori, judging from the descriptions, no specimens having been seen. They are *Uredo chrysophyllicola* P. Henn. (Hedwigia **41**: 106. 1902) and *U. Chrysophylli* Sydow (Hedwigia **49**: 78. 1909).

Uredo ignava sp. nov.

II. Uredinia amphigenous, numerous on light brown discolored areas, roundish or oblong, 0.2–0.6 mm. across, pulverulent,

cinnamon-brown; paraphyses peripheral, numerous, hyphoid, incurved, 10–13 by 29–45 μ, the wall pale cinnamon-brown or sometimes colorless, 1–1.5 μ thick, frequently thickened 3–5 μ on the convex side; urediniospores obovoid or ellipsoid, 14–19 by 23–27 μ; wall colorless or pale cinnamon-brown, 1–2 mm. thick, moderately echinulate, the pores obscure, probably 4 and equatorial.

On *Bambos vulgaris* Schrad., Santiago de las Vegas, Cuba, January 29, 1916, *J. R. Johnston 424* (type); Maricao, Porto Rico, March 15, 1916, *Whetzel & Olive 428, 429;* Mayagüez, Porto Rico, March 20, 1916, *Whetzel & Olive 427.*

The rust produces an abundance of pale yellowish sori on both sides of the leaf, but especially beneath, and more or less discolors the tissues. It has been referred to *Uredo paspalicola* (Uredinales of Porto Rico, Mycologia **9**: 92. 1917; Uredinales of Cuba, Mem. Torrey Club **17**: 165. 1918), which it much resembles. There are a number of bamboo rusts. The material listed here has been carefully compared with *Puccinia corticioides* Berk. & Br. (Syd. Ured. *1263*), *P. Kusanoi* Diet. (Syd. Ured. *1239, 1313, 1373*), *P. longicornis* Pat. & Har. (Syd. Ured. *1314*), and one other species distributed by Kingo Miyabe as *P. Phragmitis*, all from Japan, and *P. Bambusarum* (P. Henn.) Arth. from South America, as well as *P. Arundinariae* Schw. from North America, all on species of *Arundinaria* or *Bambos* (or *Bambusa* as the generic name is often written). It has also been compared with the descriptions of other species on these hosts.

Aecidium Clemensae sp. nov.

O. Pycnia epiphyllous chiefly, few, crowded opposite the encircling aecia, noticeable, reddish-brown, subepidermal.

I. Aecia hypophyllous, crowded in orbicular groups 3–8 mm. across on much larger slightly discolored spots, cupulate or cylindric, 0.2–0.4 mm. in diameter; peridium revolute, coarsely lacerate; peridial cells rhomboidal, 32–47 μ long, somewhat overlapping; aeciospores angularly globoid or broadly ellipsoid, 19–27 by 24–27 μ; wall colorless, 1–2 μ thick, moderately and closely verrucose.

On *Cissus incisa* (Nutt.) Des Moulins, Fort Sill, Oklahoma, June 19, 1916, *11931* (type), July 27, 1916, *11931a*, both collected by Mrs. Joseph Clemens. This aecial rust is undoubtedly heteroecious. It has some resemblance to the aecia of *Puccinia subnitens*

Diet., but possesses much larger spores. It is a pleasure to have the opportunity to name this rust in honor of an indefatigable and able collector, who has contributed largely to the wealth of material for study in the rusts as well as in many other groups of plants. The material has been secured from many regions during her world-wide travels, and has been most generously placed at the service of students.

Aecidium Bourreriae Holway, sp. nov.

O. Pycnia amphigenous, few in small groups, noticeable, subepidermal, 128–160 μ broad.

I. Aecia hypophyllous, loosely grouped, short-cylindric, 0.2–0.3 mm. in diameter; peridium fragile; peridial cells rhombic in side view, 13–15 by 23–24 μ, slightly overlapping, the outer wall 6–7 μ thick, transversely striate, the inner wall 3.5–4.5 μ thick, closely and rather prominently verrucose; aeciospores globoid or ellipsoid, 19–23 by 23–26 μ; wall colorless, rather thick, 1.5–2.5 μ, closely and finely verrucose.

On *Bourreria havanensis* Miers, Nassau, New Providence, Bahama Islands, March 2, 1903, *E. W. D. Holway.* Professor Holway distributed this collection under the name here used, but left the publication of the description to some one else.

Aecidium Chamaecristae sp. nov.

Aecidium Cassiae Ellis & Kellerm. Trans. Kans. Acad. Sci. **10**: 91, hyponym. 1887. Not *A. Cassiae* Bres. 1891.

O. Pycnia amphigenous, subepidermal, noticeable, in small groups, 70–96 μ in diameter.

I. Aecia amphigenous, loosely grouped upon reddish spots 2–8 mm. across, cupulate, 0.1–0.2 mm. in diameter, short; peridium recurved, erose; peridial cells rhombic or rhomboidal, 16–23 by 26 35 μ, considerably overlapping, the outer wall thick, 9–10 μ, transversely striate, smooth, the inner wa l thinner, 4–6 μ, closely verrucose; aeciospores globoid or ellipsoid, 15–19 by 18–25 μ; wall colorless, thin, 1–1.5 μ, finely and closely verrucose.

On *Chamaecrista fasciculata* (Michx.) Greene (*Cassia fasciculata* Michx.), Manhattan, Kansas, 1886, *W. A. Kellerman* (Ellis & Ev., N. Am. Fungi *1825*); Lincoln, Nebraska, May 28, 1902, *John L. Sheldon;* same, May 29, 1902, *George G. Hedgcock.* The species has apparently never been described, and the name long since chosen was already in use when given. The original collection

issued as No. 1825 in Ellis & Everhart's North American Fungi may be accepted as the type. The collections give the host as *Cassia Chamaecrista*, which by some taxonomists is considered to be the same as *C. fasciculata*. The fungus much resembles *Aecidium Torae* P. Henn., occurring on *Cassia Tora* in Ceylon and Africa, but varies in seemingly important ways, particularly in having well-developed pycnia, which are absent in the foreign collections examined.

Aecidium modestum sp. nov.

O. Pycnia caulicolous, inconspicuous, subepidermal, globoid, 160–220 μ in diameter.

I. Aecia caulicolous, in groups 4–10 mm. long, short cylindric, 0.3–0.4 mm. broad; peridium erect, erose or somewhat lacerate; peridial cells seen with difficulty in side view, in face view very irregular in shape, 19–23 by 35–58 μ, the outer wall thin, about 1–1.5 μ, almost smooth, the inner and side walls 2–3 μ thick, closely and prominently verrucose; aeciospores ellipsoid or oblong, 23–26 by 27–32 μ; wall colorless, 1–1.5 μ thick, finely and closely verrucose.

On *Zephyranthes* sp., near Ixmiquilpan, State of Hidalgo, Mexico, 1905, *Rose, Painter & Rose 8952*. The species differs from *A. Zephyranthis* Shear, also from Mexico, in possessing larger pycnia and aeciospores, and in having more delicate peridial cells.

Aecidium ingenuum sp. nov.

O. Pycnia hypophyllous, discoid, inconspicuous, subcuticular. 80–130 μ broad by 40–50 μ high, without ostiolar filaments.

I. Aecia hypophyllous, closely packed in rows, nearly cylindric to tongue-shaped, often confluent; peridium erect, 0.5–0.8 mm. high, very delicate and fragile; peridial cells in radial section narrowly oblong or linear, 10–16 by 32–42 μ, somewhat overlapping, the outer wall 1–2 μ thick, smooth, the inner wall 3–5 μ thick, closely verrucose with slender tubercles; aeciospores globoid or broadly ellipsoid, 13–16 by 16–23 μ; wall colorless, 2–3 μ thick, half the thickness being due to the close, rather fine and somewhat deciduous tubercles.

On *Picea canadensis* (Mill.) B. S. P., Fish Creek, Wisconsin, June 30, 1913, *J. J. Davis;* Solon Springs, Wisconsin, June 17, 1914, *J. J. Davis;* and Walden, Vermont, June 8, 1917, *C. L. Orton*, communicated by C. R. Orton (type). This is the first

Peridermium on *Picea* having subcuticular pycnia to be found in North America. In Europe one such form is known, which was shown by cultures made in 1916 by Ed. Fischer (Mitt. Nat. Ges. Bern **1916**: 131. 1917) to belong to *Pucciniastrum sparsum* (Wint.) Ed. Fisch., on *Arctostaphylos*. The American form doubtless belongs to some species of *Pucciniastrum*, but probably not to *P. sparsum*, as the spores are considerably smaller than in the European form of that species.

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The preparation and treatment of woods for microscopic study*

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(WITH SIX TEXT FIGURES)

CONTENTS

1. INTRODUCTION

By reason of extreme variation in the mineral, resin- or gum-like content, and in the texture, hardness, and other properties peculiar to the stem tissues of tropical woody plants, the task of preparing these for microscopic study is ordinarily a difficult one, particularly in the case of an extensive series composed of numerous unrelated species of widely differing ecological types. The published technique relating to the preparation of wood for slides has been worked out primarily from a study of the comparatively soft

* Contribution from the Osborn Botanical Laboratory.

tissues of the woods of temperate regions, to which anatomical work has, in large part, been confined. Such tissues often cut satisfactorily without treatment, while even oak and hickory, among the hardest of such woods, if taken from fresh (green) material, may be satisfactorily sectioned along any plane, by a microtome, without any preparatory treatment. Tropical wood collections, on the other hand, ordinarily embrace a high proportion of species the tissues of which, particularly when selected from dry material, can only be cut after a more or less prolonged treatment, the nature of which varies considerably according to the structural features of the species or type. Moreover, after sections of sufficient clearness have been obtained, to an even greater degree than in temperate woods, there are many anatomical characters, often of the greatest interest, which cannot be satisfactorily observed without the use of reagents, stains, or media of definite refractive properties. To meet the particular needs in this field, there is insufficient information at hand, and, further, little seems to have been added in recent years. Papers marking distinct progress in anatomical work too often neglect to publish essential details in the methods employed.

During the years 1916–1918, the writer carried out an extended investigation of the woods of Hawaii. In the course of these studies it was found necessary to devote a very considerable amount of the time to the preparation of slides, and altogether more than three thousand permanent mounts were made, including approximately one hundred macerations. In connection with this work, various accepted methods were tested and a number of new ones were devised. In the present paper, the technique employed is described in some detail, particular attention being called to certain heretofore undescribed methods of treatment and to a number of improvements on the methods in in common use. While emphasis is thus placed upon the treatment of the highly complex woody tissues of tropical dicotyledons, the suggestions embodied should be of value in the treatment of other woods than tropical, or of other than woody tissues, in that, to a certain extent, the treatment of some of the cellulose tissues of the stem, particularly the collenchyma and phloem layers, has been included.

The writer is indebted to Professors J. W. Toumey, S. J. Record and others, of the Yale School of Forestry, and to Professors A. W. Evans and G. E. Nichols, of the Department of Botany, for the use of authentic material, for the facilities essential for accurate work, and for many helpful suggestions and criticisms.

2. ADJUSTMENT OF MICROTOME

For sectioning, Thomson's modification of the Jung-Thoma sliding microtome ('10), supplied with Walb blades 170 mm. in length and 35 mm. in width, was used. To secure the best results, it was found essential that careful attention be paid both to the sharpening of the knife and to its adjustment on the carriage of the microtome. Briefly, the knife was first sharpened to a wedge-shaped edge of which the two planes were inclined at an angle θ (FIG. 1) of 20° to each other. At the same time, perfect axial

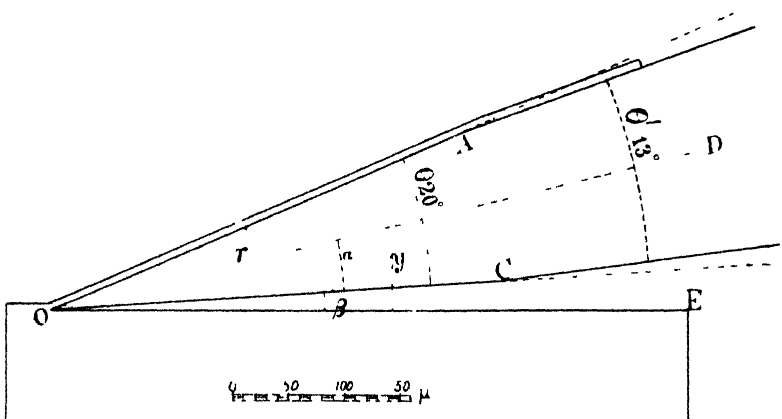

FIG. 1. Diagram to show edge of sliding microtome knife cutting section 10 μ thick. β (representing downward inclination) = 4.° θ (representing acuteness of edge after being ground with back raised by cylindrical clamp) = 20.°

alignment of the cutting edge was secured in the manner to be described presently. In mounting on the carriage, the blade was first inclined downward so as to form an angle β (FIG. 1) of 4° between the lower plane (*OC*) of the knife wedge and *OE*, the plane in which a given tissue is to be sectioned (vertical inclination). The knife carriage was then revolved in a horizontal

plane so that the edge of the blade lay at a definite angle with reference to the direction of movement of the carriage on the slide-way. For general work, a horizontal angle of inclination of about 20° was found satisfactory, but to obtain extremely thin sections, as in imbedded material, an angle of about 5° proved to be best.

Since angle θ' (FIG. 1), which the planes of the average microtome knife make with one another, is ordinarily more acute than at the edge honed to 20°, this difference must be allowed for in adjusting the vernier. Thus if θ' is 13°, the vernier should read 7.5° to give an inclination of 4°, an excellent angle for most work. A few woods containing gummy or resin-like material cut better at a somewhat greater inclination, as 6°. On the other hand, if the blade tends to "pull into" the tissue, a more acute inclination may be needed.

It is doubtful if cutting edges with θ less than 20° should ever be used in cutting woody tissues The more acute edge is too easily injured to be used in cutting many of the harder woods, such as *Pandanus*, even when these have been carefully treated. The 20° edge, on the other hand, has sufficient strength in blades of good quality to appear undamaged under the microscope after use in cutting any of the treated material, and at the same time it is sufficiently acute to meet every requirement The chief objection to using a more obtuse edge is that the section, especially at steep inclinations of the blade, is too sharply bent at O, FIG 1, in cutting, so that it tends to curl or even roll up It is partly for this reason, also, that the downward inclination of the knife (angle β) should not be greater than necessary.

But even if the inclination is correct, the quality of the work which the instrument is capable of doing may be seriously impaired by an imperfectly aligned cutting edge. This, of course, is a point which does not have to be taken into account at all in using a rotary microtome. For the sliding microtome, it is not sufficient that the edge shall coincide with a single plane, as OD, FIG. 1. Errors of alignment from heel to point may still be present by reason of which an otherwise well sharpened edge would not coincide with a plane passing through O at right angles to OD. Here an error so slight as to escape detection by the eye may be the entire cause for poor work. For example, let the error of

alignment, r, midway between heel and point be 0.3 mm. with reference to a plane meeting the bisecting plane *OD* at right angles and in contact with heel and point. Let angle $\theta = 20°$, angle $\alpha = 10°$, angle $\beta = 4°$, and angle $\alpha + \beta = 14°$. Distance $y = r \sin(\alpha + \beta)$, representing the error of alignment of the knife edge with reference to the plane of section, will then be 72 μ. In other words, when heel and point of blade are in contact with the plane of section, the edge at mid-distance will be 72 μ above this plane; whence it follows that with each full heel-to-point horizontal stroke in cutting, as when revolved horizontally at an acute angle of about 4° with reference to the direction of motion, the edge will twice traverse a vertical distance of 72 μ through the tissue, destroying the section. With the edge thus imperfectly aligned, the knife can be used to advantage in a sliding microtome only when placed less obliquely to the direction of motion than is essential for the cutting of thin sections, as at 20°–40°, in which position sections are cut with fractional strokes considerably less than the length of a 170 mm. blade.

To give the true edge essential to accurate work in cutting woody tissues, the use of a special type of hone is necessary. Such a hone consists of a piece of plate glass as wide as the knife is long, with a true plane surface covered with Diamantine Powder and oil or water, so that the knife remains constantly in contact with the hone throughout its length during the process of grinding. An excellent abrasive may be prepared by grinding two fine Belgian or carborundum hones together, and collecting the fine powder thus produced on the surface of the glass. This is not so harsh as the No. 1 Diamantine. Having ground the blade on the glass hone until the edge at both sides makes perfect contact with the surface, a brief grinding on a Belgian hone (2 x 8 in.) wet with 30 per cent glycerine will often give an edge sufficiently even and sharp for general work. The knife should be drawn across the hone obliquely, heel and edge forward, alternately upon each side. But, for best results, this grinding should be followed by sharpening upon a flat leather-surface hone, the blade in this case being pushed obliquely, point and back forward, along the hone. The surface of this hone may be kept in condition by the use of any of the fine abrasives used for this purpose on razor strops. A strop

of the hanging type should not be used in that it tends to round the planes of the knife wedge. The wedge angle is best regulated by the use of a cylindrical metal clamp fastened to the back of the knife during the process of sharpening.

In addition to the possession of (1) true axial alignment, the edge should (2) be sharp enough throughout its length to cut a hair by contact and (3) should appear perfect'y even and without nicks under the low power of the microscope. The number of sections which may be cut without re-sharpening the knife is ordinarily small; with difficult material, frequently as few as two or three perfect sections.

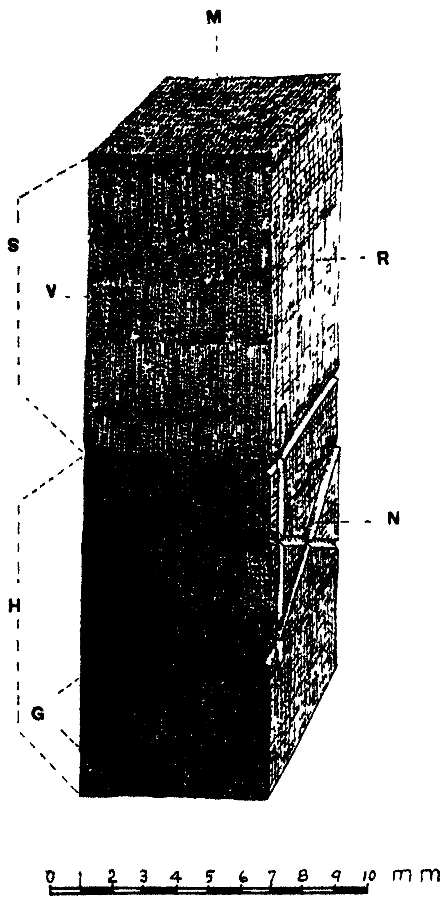

FIG. 2. Block showing tropical wood (*Tecoma* sp.) with tissues properly oriented for sectioning in cross, radial, or tangential planes. *H*, heart-wood; *S*, sap-wood. The rays (*M*, *R*) are low and narrow; the vessels (*V*), numerous and small. *G*, growth-ring.

3. PREPARATION OF MATERIAL FOR SECTIONING

A. CUTTING THE BLOCKS

In preparing material for sectioning, the blocks must be shaped with reference to the plane or planes in which the sections are to be cut. Thus a block intended for a cross, radial, and tangential series of sections may have a radial length of 2 cm., a vertical height of 8 mm., and a tangential thickness of 6 mm. Sections cut from the three planes of such a block will ordinarily include at least one full growth-ring (*G*, FIG. 2) and the full height of the

rays. Occasionally a species with higher rays or other special features may require blocks of larger dimensions. When present, both heart-wood (*H*) and sap-wood (*S*) may be included. The block should be carefully trimmed with a knife so that the tissues are perfectly oriented with respect to each of the planes intended for sectioning. The medullary rays in particular should coincide as perfectly as possible with the radial plane. In tropical woods, the rays are often narrow, visible only under a lens, and curved, so that more than ordinary care is necessary in trimming this surface.

Before proceeding with the treatment, the blocks should be numbered for sake of record. Some use a system of notches along the edges. Perhaps one of the best methods is to carve Roman numerals on the radial face not intended for sectioning, underscoring IX to distinguish it from XI (*N*, FIG. 2); also, many tropical woods require an arrow to indicate the direction of growth.

B. REMOVING THE AIR

After the blocks have been cut the desired shape, air should be extracted as far as possible from the cell lumina by alternate boiling and cooling in water. The use of an Eimer and Amend aspirator No. 3250 after boiling greatly hastens the process. This treatment should be continued until the lightest blocks sink and little or no air comes from the tissues when the aspirator is applied. Most blocks sink in a few hours, but species with numerous tyloses may take a longer time. Thus, blocks of *Rhus semialata* Murr. var. *sandwicensis* Gray remain floating five days during the boiling and cooling process, or two days when boiling periods are followed by the application of the aspirator.

C. SOFTENING THE TISSUES

Nearly all xerophytic species of tropical woods require a long treatment in strong hydrofluoric acid, often extending over several weeks, before they can be sectioned. Rain forest and bottom-land woods are frequently soft, but even such woods usually cut with clearer outlines when treated for at least a few days in acid.

For treating material with hydrofluoric acid, the blocks, after removal of air, may be placed in a wide-mouthed glass bottle, care-

fully coated inside with hard paraffin, or, still better, in cups prepared by cutting empty hydrofluoric acid bottles. Strong hydrofluoric acid is added to cover the material, and the container then corked or covered with a hard paraffin plate for a period varying from a few days to six weeks or longer, the length of time being determined by removing blocks at intervals of one to several days and testing with a sharp scalpel until they are found to be sufficiently soft to cut easily in transverse section.

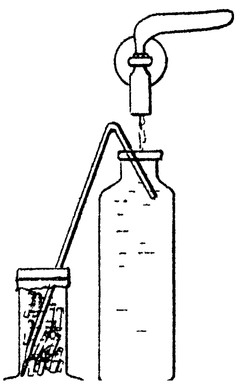

FIG. 3. Siphon apparatus for washing blocks or sections.

In the writer's experience, tissues are rarely injured by leaving them a long time in hydrofluoric acid. Thus, in case of a young stem of *Dracaena curea* Mann, delicate tissues, such as the phloem, cambium, undifferentiated parenchyma, and other thin-walled tissues, together with the bundles of needle-like raphides of calcium oxalate, were all left uninjured by long treatment in acid. In one instance, a block of *Santalum Freycinetianum* Gaud., of the size and shape described for FIG. 2, was placed in acid on September 6, 1917, and left until March 26, 1918, when it was washed and sectioned. Though in moderately strong acid for over six months, all structures, including the mineral crystals, were in perfect condition.

Hydrofluoric acid probably softens the tissues mainly, if not entirely, by the removal of silica (desilicification). But other minerals would probably be acted upon. For example, calcium would form the insoluble calcium fluoride which would remain in the wall. Curiously, crystals of calcium oxalate in crystal parenchyma or idioblasts usually remain nearly or quite intact long after the wood has been sufficiently softened to cut well. Even in maceration by Schultze's solution, crystals may be uninjured. Dr. A. J. Hill suggests that, in case of the hydrofluoric acid treatment, the crystals may have been protected by the formation of an insoluble film of calcium fluoride, the possibility of which is seen from the following equation:

$$CaC_2O_4 + 2\,HF = \underset{\text{Insol.}}{CaF_2} + H_2C_2O_4$$

The presence of such a film was indicated, though not certainly proven, by refraction tests. Another possible agency of protection may consist in a thin and presumably impermeable organic membrane closely applied to the surface of the crystal. Such a membrane may be detected by zinc chlor-iodide or by the haematoxylin stain. Also, a thicker mucilaginous membrane is usually visible outside the inner thin membrane. The resistant character of these organic coverings is indicated from the fact they may be little if at all acted upon by Schultze's solution.

As soon as the tissues have been sufficiently softened to cut well, they should be washed in running water for about four days to remove all acid. An arrangement like that shown in FIG. 3 is recommended both for this purpose and for washing the sections at a later stage. The blocks are placed in a short jar the top of which is covered with cheese-cloth through which the pointed end of a glass siphon tube is pushed. The long arm of the siphon should extend to the bottom of the jar. The short arm takes its water from a somewhat taller jar placed beneath a running tap. After washing, the blocks should be covered with glycerine where they may remain until needed for sectioning. The effect of the glycerine is such that any tissues which have become too brittle, in a few hours, become sufficiently flexible to cut well with the microtome.

D. IMBEDDING

Celloidin method.—Certain woods of peculiar structure, like *Pisonia*, in which portions are composed of very soft unlignified tissues, and other woods, in case it is desired to cut extremely thin sections, must be imbedded in celloidin before cutting. In imbedding, the general procedure followed was that described by Plowman ('04). Solutions of Schering's celloidin in a mixture composed of equal volumes of ether and absolute alcohol may be prepared in 2 x 8 cm. shell vials in concentrations of 2, 4, 6, 8, 10, 12, 14, 16, 18, and 20 per cent. The blocks to be imbedded are first treated in hydrofluoric acid and washed as above described. Next, in the usual manner, they are gradually transferred to 100 per cent alcohol. During the latter stages of this dehydration process, they are left two days in each alcohol, and the absolute alcohol is changed at least once. They are now transferred to a

mixture of ether and alcohol, in equal volumes, and finally through the graded series of celloidin solutions, being left about twenty-four hours in each concentration. On reaching the 20 per cent solution, a pressure-resisting container should be used. A brass case with screw top, such as a microscope objective box, will answer the purpose, or the corked imbedding vial may be wrapped tightly with strong cord. After adding sufficient solid celloidin to thicken the solution as much as possible, it is placed in a paraffin oven at 50–60° C. for three days. During this time, the contents of the vial are kept under pressure by the confined gases with the object of forcing the celloidin more perfectly into the tissues. The imbedded blocks are then removed, hardened in chloroform for twelve to twenty-four hours, and placed in a mixture of equal parts of 95 per cent alcohol and glycerine until ready for sectioning.

Paraffin method.—Only very soft tissues should be imbedded in paraffin. Woody tissues, even after being well softened by acid, are likely to become too hard during the process of imbedding in paraffin to cut well with the microtome.

E. SECTIONING WITH THE MICROTOME

Unimbedded material.—After softening the tissues as already described, the material is ready to section. In cutting sections, the blade of the knife should be kept flooded with a 15 per cent solution of glycerine in 95 per cent alcohol. Sections are best removed from the blade by a fine camel's hair brush and are transferred to water. From blocks prepared as above described, cross-sections may be cut as thin as 10-15 μ; radial sections, 8–20 μ; and tangential sections about 7 μ. Where, for special purposes, such as the study of the detailed structure of pit membranes, it is necessary that the sections be considerably thinner than this, the material must be imbedded in celloidin as above described.

Imbedded material.—To section material after imbedding in celloidin, the blade may be moistened either with 95 per cent alcohol or with the alcohol-glycerine mixture. Sections of woody tissues may then be cut to less than 3 μ in thickness. To obtain very thin sections, it is essential not only that the knife be sharp, but that it be ground to an alignment sufficiently true to admit of the use of the blade at very oblique horizontal inclinations with refer-

ence to the direction of motion, such as 4°. Thin sections such as these require great care in handling. In most cases, particularly in the longitudinal planes, only extremely small pieces may be cut, since such sections, being less than the diameter of the cells, are often sections of single cells and may even be too small to be seen without a lens.

After washing the sections in water to remove all glycerine, the celloidin may be removed by covering the sections for several hours with the ether-alcohol mixture. The process of clearing may go on very slowly and more than twenty-four hours may be required to remove all celloidin. The sections should now be placed on a slide in dilute albumen fixative (one drop to 2 c.c. of distilled water) and warmed slightly until dry. After standing over night, they are ready for staining. For staining, Koplin jars are best used, but otherwise the procedure is the same as for unimbedded material to be described in connection with differential stains.

F. FREE HAND SECTIONS

Since small unstained radial and tangential sections mounted in glycerine ordinarily show the essential anatomical features, the following method, though especially adapted to coniferous woods, is suggested, in connection with macerated preparations, to assist in the rapid identification of material. The radial and tangential surfaces are first cut true with a knife, then a sharp razor is drawn lightly over the surface allowing it to cut thin fragmentary pieces. These are placed in a drop of water on a slide and held over a flame until boiling temperature is reached. Alcohol is now dropped upon the section until all air has disappeared from the cell-lumina. After a brief staining in aqueous potassium iodide solution of iodine, the sections are ready to mount in glycerine.

4. PREPARATION OF MATERIAL BY MACERATION

Many tropical woods contain substances in the ray cells and in other elements, by reason of which details of pitting and similar features are obscured. Macerations will be found satisfactory in such instances and the following modification of Schultze's method is suggested for their preparation:—

1. Cut chips to expose a radial length of 2 cm., an axial length of 1 cm., and a tangential thickness of 2 mm.

2. Place these in a numbered test tube, cover with water, and keep at boiling temperature in the water bath for about an hour. The hot water is then replaced by fresh cold water and the tube reheated. Alternate cooling and boiling periods should be continued for at least five changes.

3. Cover the material with 50 per cent nitric acid and add a small amount of potassium chlorate (as much as may be taken upon the point of a small knife blade). It is now kept at boiling temperature until the pieces have whitened and commenced to fray, when cold water is poured on, causing the macerated material to settle. The acid solution is then replaced with water and allowed to heat with the purpose of removing the acid solution.

4. Transfer the material to a watch-glass where it may be teased apart with a small size artist's brush. By means of a pipette, change the water several times or until all particles of foreign matter and traces of chemicals have been removed.

5. Replace the water by 95 per cent alcohol for 30 minutes or until all air has been removed from the cell-lumina.

6. Replace the alcohol by a 2 per cent solution of Bismarck brown in 70 per cent alcohol, in which the material should stand for twelve to twenty-four hours.

7. To remove excess stain, wash quickly in alcohol and transfer to glycerine, which should be changed if greatly colored by the stain.

8. Mount in glycerine and cement with Brunswick black or gold size.

Preparations such as these are almost essential for the working out of the details of vascular anatomy. If a water bath capable of receiving twenty test tubes is used, but little time need be consumed in making the preparations. The action of the chemicals proceeds so slowly that there is little danger of tissues being destroyed.

5. DEFINITION OF ANATOMICAL DETAILS

A. BY DIFFERENTIAL STAINING

In the writer's experience, Haidenhain's iron-haematoxylin has proved the best all-round stain for bringing out the anatomical

structure of woody tissues. This is true both for the relatively thick sections cut from unimbedded blocks and for the very thin sections obtained by the celloidin method. In these latter sections, for example, it is possible with this stain to bring out such structures as the reticulated thickenings of pit membranes as well as similar features not visible by other means.

Before staining, sections cut from the unimbedded blocks or imbedded sections on slides are washed in three or more changes of water to remove glycerine. The sections are then covered with a 2.5 per cent aqueous solution of iron-alum (ferric ammonium sulphate) for five to twelve hours. Next, they are washed in running water for five minutes (or two minutes in case of slide material), stained with 0.5 per cent aqueous solution of haematoxylin (Chamberlain, '15, p. 41) for twelve to twenty-four hours, washed in water for three minutes, and then again treated with the iron-alum solution. The sections are left in the iron-alum until they become light gray, but, for best results, the material should be watched under the microscope, so that the process may be stopped the moment the clearest definition is reached. Sections are then washed in running water for three hours or longer to remove all trace of iron-alum. In many cases, this washing also serves to remove precipitates and other clouding matter from the tissues so that the clearness and transparency of the section is greatly improved. It is often well to extend the period of washing to twenty-four hours or longer. For this purpose the siphon apparatus shown in FIG. 3 is useful, since it allows a thorough percolation of water through the sections for any length of time without danger of mechanical injury to the tissues or of loss of material. The sections rise flat to the top directly in the outflowing tap water which, from a public supply system, is usually sufficiently alkaline to give a clear blue color to the haematoxylin, hence being preferable to distilled water for this purpose.

For best results, woody tissues stained as above should be counterstained with safranin. This stain is made up by combining equal portions of a 1 per cent solution of alcohol-soluble safranin in 95 per cent alcohol and a 1 per cent aqueous solution of water-soluble safranin. For extremely thin membranes, where a very weak counterstain is desirable, one to three minutes in the safranin

may be sufficient; but for general work, longer periods up to two hours, giving a heavy but not too opaque stain, are desirable. Dehydration is accomplished by washing quickly in 95 per cent alcohol, then successively in absolute alcohol and xylol. The sections are mounted in dammar or balsam.

Sections which tend to curl badly after cutting, as in case of many woods with thick-walled elements, may be placed, as soon as cut, between two glass slides and allowed to dry before staining. In most cases, the section may then be placed free in the stain, but occasionally it may be necessary to proceed with one or more steps of staining before removing from the slides.

For a number of purposes, the above process, with slight modification, may be used successfully in staining the soft cellulose tissues of the bark; but for this purpose Congo red is superior to safranin as a counterstain. Where shrinkage due to dehydration is not too great and the cell contents stain black, as in *Malus* or *Pyrus*, preparations showing clearly such details as the reticulate thickenings, pits, and even protoplasmic bridges through the pit-membranes of the hypodermal collenchyma may be obtained by the following process:—

1. Sections 6 μ in thickness are cut from green material collected in winter, to show pits and protoplasmic bridges in section, or 10 μ in thickness to show pits and reticulations in surface view.

2. Place for five hours in 2.5 per cent aqueous solution of iron-alum.

3. Wash five minutes.

4. Stain about twelve hours in 0.5 per cent aqueous solution of haematoxylin.

5. Wash five minutes.

6. Differentiate in a 2.5 per cent iron alum solution until sections are gray.

7. Wash three hours.

8. Stain in a saturated aqueous solution of Congo red one to five minutes for pits in section, ten to thirty minutes for pits in surface view, one to two hours for reticulation of thin end-walls.

9. Dehydrate in absolute alcohol one minute.

10. Clear in xylol one minute.

11. Mount in dammar.

Also, longitudinal sections of phloem 6 μ in thickness, when treated as above, will show the lattice-like arrangement of sieve areas in the lateral walls of the sieve tubes.

A convenient method of numbering and labeling slides is as follows. By means of a camel's hair brush, cover the entire upper surface of the slide outside the coverslip with dilute dammar (mounting consistency diluted twenty to thirty times with xylol). The brush is best fixed in the cork of a bottle used to contain the solution. In a few seconds the records may be written with Higgin's waterproof ink, and index arrows sketched to point to any special part of the mount, if desired. The surface should then again be brushed with dammar that the slide may be freely handled or washed without injury to the writing.

B. BY DIFFERENTIAL REFRACTION

The laws of refraction may be employed not only to give clear definition to details in outline, but also to determine physical or chemical qualities of cell-walls or cell-contents. In either case characters may often be determined by refraction more readily and with greater precision than by the reaction of stains or of chemical reagents. Refraction opens a wide field for research in plant histology and will be treated in some detail in a subsequent paper dealing with refraction of light in relation to plant tissues.

6. MICROCHEMICAL REACTIONS

Characters readily observed by microchemical means often have a systematic value, or are of ecological or physiological interest, or are closely identified with the peculiar qualities of color, hardness, hygroscopicity, porosity, durability, strength and other properties upon which depends the special value of any given wood in the arts. In the following paragraphs are indicated several important characters frequently found in woody tissues of warm climate trees, together with a number of microchemical tests helpful in connection with their demonstration.

A. CELLULOSE

Sections are placed twelve hours or longer in a solution made by adding one drop of concentrated aqueous Congo red to 20 c.c.

of distilled water. Cellulose tissues turn deep blue as soon as transferred to 10 per cent hydrochloric acid. If mounted in glycerine (acidulated by adding one drop of strong hydrochloric acid to 10 c.c. of glycerine) and well cemented with Brunswick black or gold size, the blue color will remain several months without fading.

B. CELLULOSE-LIGNIN

The above test for cellulose may be varied by transferring the section for a brief period to a strong aqueous solution of anilin chloride immediately after the treatment with Congo red, the remainder of the treatment being the same. Lignified tissues appear yellow; cellulose, blue.

C. GUMS

Gummy substances, both those which are soluble in water and those which swell without going into solution (mucilages), are constantly met with in woody tissues, occurring in the lumina of vessels, tracheids, and other cells, or in intercellular canals or cavities, these latter resembling resin cavities. Certain forms of each (gums and mucilages) are believed to play the rôle of reserve material (Haas and Hill, '13, p. 125; Grüss, '96). Fibers, composed in large part of mucilaginous inner layers, are also of frequent occurrence. The gummy nature of amorphous bodies observed in permanent mounts is usually indicated by shrinkage checks or other evidences of contraction on dehydration, as in FIG. 5 (see further below). Gums may be further distinguished from resins by their insolubility in chloroform.

Mucilaginous laminae in fibers ("gallertartige Verdickung" Sanio, '63, p. 105; Solereder, '08, p. 1143: "Hemicellulose," Grüss, '96; Schellenberg, '05: "cellulose," Potter, '04: "mucilaginous fibers," Sachs, '75, pp. 35–36; Jeffrey, '17).—Frequently woody fibers, particularly of xerophytic species, are composed of one or more clear, gelatin-like concentric inner layers which shrink greatly on drying (FIG. 4); in young tissue, they turn deep violet with zinc chlor-iodide. Solereder ('08, p. 1143) records twenty-two families in which such fibers occur, and his list is not complete. In a given wood, fibers of this description may occur either sporadically or in regular distribution;

they may be few in number or may compose nearly or quite 100 per cent of the prosenchyma. In some cases (*Robinia*), the purple reacting lamellae of fibers may function as reserve material, and be more or less completely dissolved in the growing season (Schellenberg, '05; Grüss, '96). In this connection, twigs of *Acer rubrum* L., *Cercis canadensis* L., and *Robinia Pseudo-Acacia* L., gathered in winter condition, sectioned, and treated with zinc chlor-iodide, make favorable material for study. A number of distinctive properties are exhibited by such fibers:

a. Hygroscopicity.—Mucilaginous layers readily take up water, swell without going into solution, and shrink correspondingly on

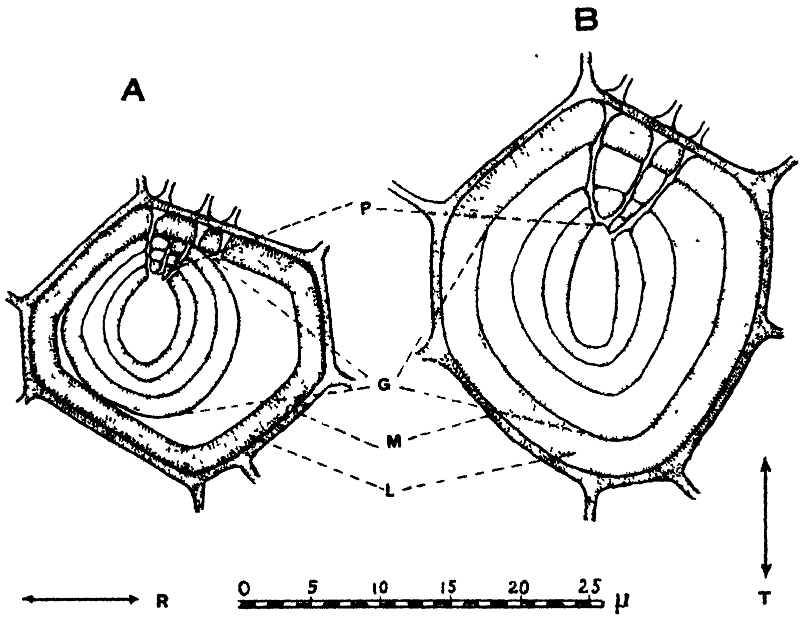

FIG. 4. Abbé camera drawings of a laminated fiber of *Xylosma hawaiiense* Seem. in cross-section. *A*, after desiccation. *B*, after treatment with water. All layers have swollen, but the mucilaginous layers (*G*) more than the ligno-cellulose outer portion (*L*). The simple pits (*P*) come into alignment after soaking. One of the pits remains permanently in connection. *T*, tangential direction. *R*, radial direction.

drying. If cross-sections 15–30 μ in thickness are mounted on a slide in water, then dehydrated by flowing absolute alcohol beneath the coverslip, the mucilaginous layers may be observed to shrink greatly, in the majority of cases, drawing away from the

thin outer ligno-cellulose layer usually present (FIG. 4, *A*). Fibers in which the mucilaginous layers remain in contact with the outer layers on drying ordinarily show large shrinkage checks extending radially outward from the center, through the mucilaginous portion. Dehydration may be completed by placing the slide upon the water bath for a few seconds. In stained sections mounted in balsam or dammar, mucilaginous membranes are usually shown in the contracted state. In glycerine, water, or other media in which the tissue has been mounted without dehydration, the mucilaginous layers appear in the swollen condition. Abbé camera outline sketches of single fibers before and after dehydration, made with high power and extended draw tube to obtain the greatest possible enlargement, accurately show the amount of shrinkage as in FIG. 4, *A* and *B*. The mucilaginous core of such fibers often contracts over 25 per cent of both radial and tangential dimensions on drying, and swells rapidly to original size on admission of water. The outer ligno-cellulose layer and the middle lamella (*M*) which is here indistinguishable from the primary thickening of the fiber, on the other hand, show relatively little change in dimensions. The shrinking and swelling of the mucilaginous thickenings is partly independent of the other parts of the tissue, so that, as in the case of the Hawaiian woods examined by the writer, the wood tissue itself was not observed to swell or shrink in proportion to that of the mucilaginous layers of the fibers. However, blocks of wood in which mucilaginous fibers were abundant, as, for example, *Xylosma*, were found to shrink as much as 12 per cent tangentially and 7 per cent radially on drying from saturation.

b. Reaction to stain and other reagents.—Stains and chemical reagents react differently according to the age of the tissue; also, after material has been softened in hydrofluoric acid, neither stains nor chemical reagents give characteristic reactions.

In old tissue (heartwood), haematoxylin, Bismarck brown, and anilin blue stain the mucilaginous layers with varying intensity as a substance of variable composition. Very commonly stains, particularly the safranin, are readily extracted by the alcohol washes or other treatments in the staining process, so that the mucilaginous layers appear slightly or not at all stained in the

finished mount. With phloroglucinol and hydrochloric acid, a more or less pronounced red reaction is usually obtained; with zinc chlor-ioidide, a yellow, brownish, or sometimes purplish color.

In young tissue (twigs, sapwood), the mucilaginous membranes stain deeply with haematoxylin, or Congo red; with zinc chlor-iodide they turn deep purple or violet.

c. Fracture.—In maceration, mucilaginous fibers are usually extremely brittle. A fragment ordinarily shows conchoidal fracture across the mucilaginous core. Woods in which mucilaginous fibers are abundant are likely to be brittle.

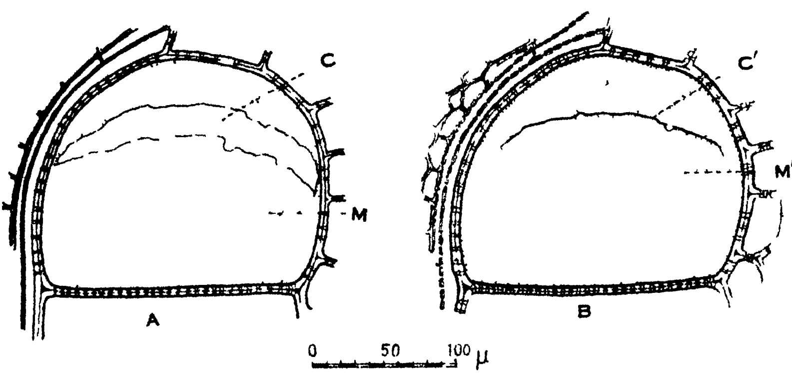

FIG. 5. Abbe camera drawings of vessel in *Tabebuia chrysantha* Nichols, (?), showing surface of insoluble gum (mucilaginous) plate (*M*). *A*, after dehydration; *B*, after admission of water beneath coverslip. The shrinkage crack (*C*) closes in *B*.

Mucilage or insoluble gum in cells, vessels, or canals.—The mucilaginous or gummy substances, which occasionally fill certain cells, vessels or intercellular cavities in dicotyledonous woods, respond to water tests in much the same way as the mucilaginous portion of mucilaginous fibers. Here the substance does not ordinarily pull away from the sides of the cavity or canal on dehydration, but cleaves apart in long wide gaps extending, usually, across the center. Such shrinkage cracks may be observed to close up tightly soon after admitting water at the edge of the coverslip, and drawing it through by means of blotting paper at the opposite side (FIG. 5). The water test serves also to distinguish the gums or mucilages from the resins, which, though they may shrink on dehydration, do not swell in water.

D. ESSENTIAL OILS, RESINS, AND GUM-RESINS

Substances of this description occur abundantly in woody tissues of tropical dicotyledons, in the cell lumina or in intercellular canals (Guignard, '92; Record, '18), in the form of globules, transverse plates or irregular masses. As before indicated, such substances may readily be distinguished from the gums by the fact that after drying they do not swell in water; also, by their solubility in chloroform. The gum-resins, however, may have some of the properties of each component. To determine the solubility in chloroform, sections (particularly those from seasoned blocks) should remain twenty-four hours in the solvent.

The essential oils, which often possess an aromatic odor, resemble the resins except that such bodies readily dissolve when absolute alcohol is drawn beneath the cover glass.

E. FATS

The fatty oils resemble, in appearance, the essential oils with which they often occur in the same cell. Both are stained by Sudan III. The fatty oi's are distinguished from essential oils from the fact that absolute alcohol dissolves few fatty oils, but does dissolve the essential oils; strong potassic hydrate saponifies fatty oils, but not essential oils, although some complex resins which break down into a fatty component may appear to be saponified; a temperature of 130° C. volatilizes essential oils but not the fats.

F. TANNIN

The presence of tannin in tissues is readily demonstrated by familiar tests. A bluish or greenish black is caused by a neutralized solution of ferric chloride, and a reddish yellow by ammonium molybdate.

G. MINERAL CRYSTALS

Vertical strands of short cells, each with a single crystal of calcium oxalate nearly filling the cavity, are of frequent occurrence in tropical woods, being found in over 26 per cent of the Hawaiian woods studied by writer. Less frequently they occur in ray-cells and other tissues. Their composition is determined from the fact that calcium oxalate dissolves without effervescence in

hydrochloric acid, but is unaffected by acetic acid. Calcium carbonate, which is of comparatively rare occurrence in crystalline form, dissolves in either acid with effervescence.

The fact that each mineral crystal is often closely incased in a resistant, nearly impermeable membrane may make it necessary to free the face of the mineral from its coating before the test can be applied. This may be done by holding a thin section in a pair of forceps, igniting, and allowing to burn or char only sufficiently to free the crystal, or a portion of it. Care must be exercised, for the calcium oxalate, with sufficient heat, is changed to calcium ca bonate and finally to calc'um oxide.

H. CHEMICAL GROWTH-RINGS

Some woods without any visible structural growth-rings, may yet exhibit what appear to be definite seasonal variations in the chemical composition of the wood, so that distinct chemical rings

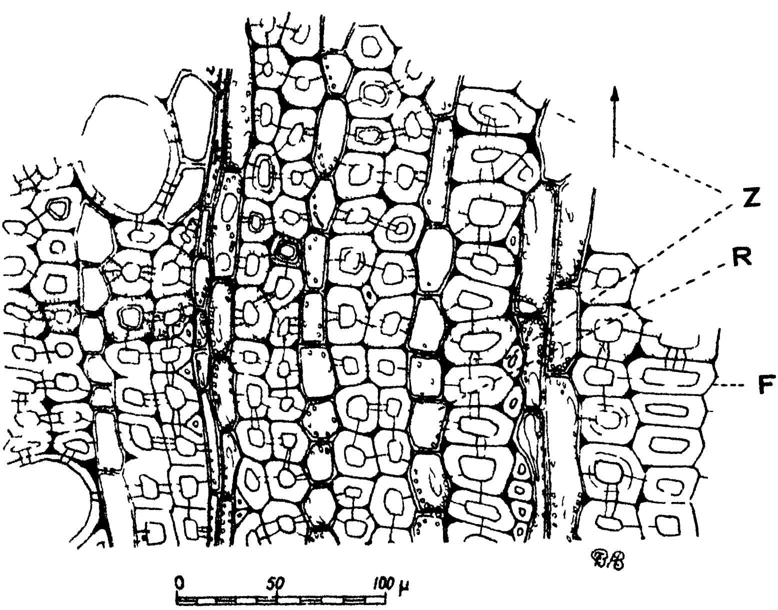

FIG. 6. Chemical growth-ring in *Xylosma hawaiense* Seem. Arrow indicates direction of growth. *Z*, lignified zone. A slight retardation of growth is indicated by somewhat shortened ray-cells at *R*, and occasional slightly compressed fibers (*F*).

may be demonstrated by microchemical means. The term chemical growth-rings is here suggested for such zonal variations in the

cellulose, lignin, mucilage, or other components of the cell-wall, which appear correlated with seasonal growth. The evidence that such zones of chemical variation actually represent true growth-rings is not without structural confirmation. For example, on following carefully a chemical ring (FIG. 6) which appears sharp on its outer face, as in *Xylosma hawaiiense* Seem., such evidences as the presence of short ray cells (*R*) or slightly flattened fibers (*F*) would seem to indicate a slight retardation of growth at that place.

In case of woods in which chemical rings are present due to seasonal variations in lignification, such rings are readily demonstrated by placing cross-sections 15–20 μ thick in an alcoholic solution of phloroglucinol for two minutes, then treating with strong hydrochloric acid. Definite chemical rings appear, which are sharply defined on the outer face, blending gradually into deeper shades toward the interior. Similarly, the cellulose test may reveal zonal differences in the amount of cellulose. Another type of growth-ring is defined by seasonal zones of mucilage-reacting fibers, but such zones, though occurring in regular zonal alternation, may not be sharply defined on either face. In *Alphitonia excelsa* Reiss., such mucilaginous chemical rings are plainly visible without a lens.

7. LIQUID PENETRATION TEST

It not infrequently happens that tyloses, gums, and other bodies which may fill the lumina of vessels and other conducting elements in the region of the heartwood, are displaced or lost during the process of sectioning or staining, so that, from a microscopic examination, one may fail to make an accurate estimate of their presence or abundance. The following test is of material aid: Alcohol is dropped upon the transverse surface of a dry block of wood. If tyloses, gums, or other bodies are abundant, the liquid spreads out over the surface; if absent, the liquid quickly disappears in the tissues and soon runs through to the opposite end. Thus, in case of the red oaks, only a few seconds are required for the liquid to appear at the opposite end of blocks six inches or more in axial thickness. Woods, in general, separate rather definitely into two classes, those which are penetrable and those which are not.

8. SUMMARY

In cutting thin woody sections with a sliding microtome, it is essential, for accurate results, that careful attention be paid to sharpening and adjusting the knife. The blade must be ground to perfect axial alignment. The wedge-shaped edge should have an angle of approximately 20°; for general work this gives better results than a more acute edge.

In softening tissues of tropical woods for sectioning, strong hydrofluoric acid may be used in preference to weak. The length of time required to soften tissues of tropical woods varies from a few days to several weeks, little if any injury being done to the tissues by remaining a long time in acid. The process of demineralization of the cell-wall may be completed without perceptible effect upon the outline of the calcium oxalate crystals contained in the cells, beyond the fact that the refractive properties may be changed.

In the maceration of woody tissues, Schultze's method may be employed with safety if equal volumes of acid and water are used.

Fibers with one or more mucilaginous inner layers are frequent in the xylem of tropical trees. Perhaps the most constant properties of the mucilaginous layers consist (1) in their marked swelling in water and (2) their brittleness on drying. With stains and reagents, reactions differ with the age of the tissue. Thus in young tissue (twigs, sapwood) gathered during the period of rest, a purple color is obtained with zinc chlor-iodide; haematoxylin, anilin blue, or Congo red stain deeply. In old tissue (heartwood), the mucilaginous layers react, as a rule, yellow or brownish with zinc chlor iodide, and take stains irregularly. Woods in which mucilaginous fibers are abundant may shrink greatly on drying or swell correspondingly on wetting, though not to the same degree as the mucilaginous membranes.

Woods without structural growth-rings may possess chemical rings demonstrable by microchemical means.

YALE UNIVERSITY

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INDEX TO AMERICAN BOTANICAL LITERATURE

1917–1919

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Mucilage or slime formation in the cacti

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(with plate 8)

The cellular processes involved in the formation of plant slimes, of gums, and of resins are subjects which have attracted the attention of many investigators.

Pfeffer (16) in his "Physiology of Plants" states in general that mucilage may be formed by synthesis or by decomposition as when the cell wall becomes mucilaginous. He also accepts the doctrine that mucilage is often formed in the interior of the cell. Karsten (7) claims that the formation of cork, gum, slime, etc., is due to processes of intussusception going on in the protoplasm. Tschirch (21) has emphasized the conclusion that in the cell wall there is a specialized layer next the cuticle which he calls the resinogenous layer and in which so-called secretions are formed.

Of the earlier investigators, Cramer (2), Von Mohl (22), Nageli (15), Hofmeister (6), Wigand (24), Schlacht (17), Frank (4), and De Bary (3), were of the opinion that mucilage building is a disorganization process occurring in the cell wall. The transformation into mucilage they all agreed began in the outer part of the wall and worked toward the inside. Hofmeister (6) believed that the cell walls became thickened by the apposition of new layers, hence the striated appearance of the jelly. Frank (4) found that in the bulbs of orchids mucilage developed from the cell contents in a crystal-bearing cell about a bundle of crystals which finally disappear. In other plants he thought the gum was formed

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from the cell wall. He noted that at first these gum cells contained starch grains, many of which appeared corroded.

Prillieux (17), in the gummosis of fruit trees, claims that gum may appear in cells whose walls do not show a trace of disorganization. The starch grains simply disappear and small masses of gum take their place. Haberlandt (5), in his treatment of the anatomy of cells containing slime from a morphological viewpoint, considers the slime masses in Malvaceae, Marchantiaceae, Cactaceae, and Lauraceae to be a very strongly thickened and finely stratified cell membrane. According to Haberlandt (5), in such cases the primary cell wall, as a rule, does not degenerate.

In 1893 Walliczek (23), working under Tschirch, concluded that there were cell content slimes as well as membrane slimes, but that cell content slime had been proved only for *Orchis* and *Symphytum*. He found that the cell content slimes appeared as homogeneous masses, while the membrane slimes were stratified. The following year Schilling (19), working on the question of slime formation in water plants, decided that slime building went on at the expense of the cell wall and that at the end of the process only a very thin shell was left about the cell.

Butler (1), studying gummosis in fruit trees, accepts the view that the process of gum formation is a degeneration of the cell wall. The essential factors are relative rate of growth and water supply. Dissolution begins in the secondary lamella and almost coincidently in the primary membrane, and the cell contents are at no time actively concerned in gum formation.

We now turn to a consideration of the investigations that have been made relating to the formation of mucilage in the cacti. These plants have been rather exhaustively studied for many years but so far comparatively little cytological work has been done upon the group. In most of the forms mucilage is very abundant. The question as to the method of its formation was discussed first by Meyen (14) in 1837. He reported that he found mucilage in the intercellular spaces of the cacti and in some cases he found mucilage ducts in great numbers. He concluded that a direct transformation of cell contents into mucilage took place and showed a figure with cells filled with mucilage.

Two years later Schleiden (20) published the results of the

first attempted cytological study of the cacti. He noted that the contents of the parenchyma cells was primarily "starch or mucilage in globules." Both were almost always surrounded with chlorophyll. In almost all species which he studied he reported that he found two to six times enlarged cells distributed in the cortex and in the central parts of the stem, all of which were totally filled with a vegetable jelly with a characteristic type of organization. These mucilage-filled cells he said he could not find in *Rhipsalis rhombea*, but in their place he found large cells filled with starch.

Between this work of Schleiden (20) in 1837 and that of Lauterbach (8) in 1889, no very full study of the mucilage of the cacti is reported. Cramer (2) described the slime of the cacti arising as a thickened layer on the cell wall, thus proving, as he held, its close relationship with cellulose. He found these continuous thickening layers in especially large single cells. He believed that by rupture the wall layers became irregular and showed such a structure as Schleiden (20) described.

Schacht (18) studied old stems of *Opuntia Ficus-indica* and reported gum-like tragacanth contained in canals. He believed that this gum arose as the result of a disorganization of the cell wall. Wigand (24) observed that certain parenchyma cells in the cacti, which were of somewhat greater diameter than their neighbors, were filled with a homogeneous colorless slime. De Bary (3) noted that this mass of mucilage had the structure of a very thick, abundantly, and delicately stratified cell wall. He concluded that it was the cell wall thickened at the expense of the internal cavity of the cell.

From his investigations Lauterbach (8) was led to believe that there are two methods by which the mucilage is formed, one holding true for *Opuntia*, and the other for the remainder of the cactus groups. In the *Opuntia* the mucilage arises in a cell containing a small crystal of some oxalate. This crystal, as he thought, seemed to stimulate the growth of the cell. Later the nucleus and crystal might appear suspended on strands of cytoplasm in the midst of the cell and mucilage would then begin to appear in the periphery of the protoplasm.

In the other cacti he held that the mucilage also arose in the

periphery of the protoplast in the plasma membrane, but that no crystal was present. The cytoplasm is pressed toward the center of the cell as the mucilage increases until it remains as a mere remnant in the interior. By the use of a strong sugar solution he was able to make the mucilage surrounded by its delicate plasma envelope pull away from the wall. He observed striations in the mucilage, but made no attempt to account for their origin.

Walliczek (23) claims that the mucilage of the cacti arises as a secondary thickening of the primary cell wall. He also states that it does not give a cellulose reaction in the moment of its formation nor later. He suggests that the stratification in most cases is dependent upon a different water content in the layers. This stratification, he says, shows best when the material is preserved in alcohol and water added later.

Longo (11, 12) holds that the peculiar structure of the mucilage which Walliczek describes is due to the action of the alcohol which, he believes, withdraws water from the mucilage. He used fresh material as well as alcoholic preparations and found that the mucilage was not the result of a transformation of the cellulose membrane, but came from the protoplasm, showing the characteristics of mucilage as soon as it appeared. He does not agree with Lauterbach (8) that the mucilage is produced in droplets in the parietal protoplasm. He finds it appearing between this and the thin cell, wall of cellulose, which never undergoes any modification.

As to whether the mucilage arises from the wall or from the protoplasm, the opinions seem to be about equally divided, but Walliczek, Lauterbach, and Longo all agree that it is accumulated between the plasma membrane and the cell wall. In this connection I might say that in the present paper I have figured a case in which the wall between a mucilage cell and the neighboring cell shows the middle lamella with the wall of equal thickness on each side of the lamella, which is good evidence that the wall is not affected by the formation of the mucilage.

For the most part I have studied *Rhipsalis rhombea* (from the New York Botanical Garden), the species in which Schleiden (20) said he could not find any cells filled with mucilage. Owing to the incompleteness of his record it is impossible to determine whether

or not his *Rhipsalis rhombea* was identical with the species which I used. My plants are all from greenhouse sources and were probably introduced from Europe. Besides *Rhipsalis rhombea*, I have used *Rhipsalis pachyptera* and *Rhipsalis Houlletiana*, brought from France, likewise *Opuntia inermis* and *Pereskia Pereskia*.

In the leaves of the flower buds of *Opuntia* and of *Rhipsalis*, the mucilage cells are often so large and so numerous that in cross section these leaves seem to be almost filled with mucilage. With the Flemming triple stain the mucilage is colored blue, but is not so deep a blue as the starch grains. The mucilage is never, with the method I have used, of the same color as the wall surrounding it.

In the flower buds of *Rhipsalis* the large mucilage cells are abundant, not only in the floral leaves but also in the ovary wall, in some cases almost every cell being filled with mucilage. The mucilage cells are more numerous in the periphery than toward the center. Sections were made also of very young *Rhipsalis* stems. In these meristematic tissues there are numerous mucilage cells which are two or three times as large as the neighboring cells. The adjacent cells (FIG. 1) are typical vegetative cells containing a large central vacuole surrounded by a thin layer of cytoplasm adhering to the cell wall. In it are suspended the nucleus and a few starch grains.

On the other hand, in the large cell (FIG. 2), before any mucilage appears, the cytoplasm is much more dense. While it is spongy and vacuolated, there is no large central vacuole, neither is there any starch as a rule. The cells at this stage contradict entirely the possibility suggested by Lloyd (9) that their large size is due to imbibition of water by the mucilage which they contain. In the species studied by me, the cells destined to form mucilage reach a diameter two or three times that of adjoining cells before the mucilage begins to form in them. In FIG. 3 the protoplast is surrounded by a layer of mucilage, but its diameter inside the mucilage layer is approximately the same as that of the protoplast in Fig. 2.

The growth in these cells at this stage is true growth and not at all a mere matter of increased water content of a central vacuole.

As noted, their cytoplasm is especially dense and their nuclei and nucleoles proportionately large and very highly stainable, as shown in FIGS. 2 and 3. Their growth is plainly a matter of the accumulation of largely increased amounts of protoplasm preparatory to their secretory activity in the production of mucilage. While there is plenty of evidence for believing that the cells increase in size during the period of mucilage production and possibly after they are completely filled, their increase in size before there is any evidence of the presence of mucilage in them is equally clear. A glance at FIG. 2 will show the number of cells which adjoined this large cell and will give some idea of how these hypertrophied cells, which are to form mucilage, compare in size with their neighbors. FIG. 1 shows one of the ordinary cells adjoining a mucilage cell.

The mucilage or slime appears first as a very thin homogeneous film lying between the cell wall and the cytoplasm (FIG. 3). It stains but slightly and nowhere shows any conspicuous colloidal organization. In some of the older cells this layer persists about the periphery, while the remainder of the mucilage looks somewhat fibrillar and is also vacuolated (FIG. 5); in other cells the strands and vacuoles extend almost to the cell wall (FIG. 4).

As the amount of mucilage increases the cytoplasm is apparently crowded in toward the center of the cell, the nucleus and nucleole become smaller (FIG. 4), and while this is taking place both cytoplasm and nuclear-plasm become denser and lose their characteristically differentiated structure. Finally the nuclear membrane disappears and also the nucleole as such and the nuclear-plasm becomes merely a denser mass within the compressed and granular cytoplasm (FIG. 5). In the end nothing remains of the protoplasmic contents of the cell but an irregular highly stainable mass in about the middle of the cell. Sometimes this mass appears in section as a rather straight line, sometimes it has in section the shape of the letter Y. Many cells are also found which show no remnant whatever of the cytoplasm.

In the cells which are completely filled or nearly so, without exception the mucilage has the organization of a spongy substance full of vacuoles. Between and through these vacuoles there extend films, strands, or even threads, which radiate outward from

the cytoplasm in a rather characteristic fashion (FIG. 4). In some cells the mass of mucilage is rather homogeneous throughout, in many others it is reticulated and zoned (FIG. 7), so as to have led some investigators to believe that it is the much thickened and stratified cell wall.

While the cytoplasm with its included starch disappears entirely the cell wall nowhere shows a breaking down or disorganization. At the end of the process it is just as thick as at the beginning. In favorable cases the middle lamella is discernible and in such preparations the secondary wall is seen everywhere intact and is just as thick and no thicker on the side of the lamella next the mucilage cell than on the opposite side (FIG. 6). This would seem to show that the wall does not become disorganized or changed in any way as the formation of mucilage proceeds. The evidence all seems to point in one direction, namely, that mucilage in the cacti is formed not at the expense of the cell wall, but at the expense of the cytoplasm and nucleus. Neighboring cells, as well as the mucilage cell, perhaps, contribute of their content. They at any rate become flattened and contain very little cytoplasm (FIG. 5).

Haberlandt (5) has pointed out that in many cases slime containers may serve as water reservoirs and that it is not necessary to regard such slimy cell content as a useless excretion. He notes that the early differentiation of the slime cells in the vicinity of the growing point appears to point to their having a mechanical function in the growth process, and suggests that we have to do here with "Schwellapparaten."

This observation is perhaps borne out by experiments by MacDougal and others at the Tucson laboratory. It will be recalled that in his work on colloid hydratation and growth in the cacti, Long (10) reported that, in general, growth and swelling paralleled each other rather closely. Later MacDougal (13) found that agar, composed of pentoses presumably having some qualities identical with those of the plant mucilages, and both young and old disks of *Opuntia* will swell more when placed in distilled water or an alkaline solution than when placed in an acid solution. He found also that the apical parts of joints showed greater capacity for absorption than the basal portions. In a series of similar imbi-

bition experiments with joints of *Rhipsalis*, I have found that the greatest swelling in a majority of cases takes place in the apical region, the region of growth and of abundant mucilage cells.

We have then in the cacti a transformation of the content of many cells in the growing regions into a mucilage which, by absorbing water, may simulate true growth and may be of importance in conserving and regulating the supply of water for the growing cells themselves. As to the method of formation of the mucilage, as I have noted it in the cacti and more particularly in *Opuntia* and in *Rhipsalis*, it is the nucleus and cytoplasm that are the active agents. Apparently the cell wall is at no time involved in the process. The mucilage comes from the cytoplasm and the formation begins between the cell wall and the protoplasm, as Longo (11, 12) points out. As the mucilage increases the nucleus and cytoplasm decrease in size and may entirely disappear, leaving the enlarged cell completely filled with mucilage.

That all resins, gums, and mucilages are similarly formed is in no sense suggested, but it is of interest that we have in these mucilage cells of the cacti a method of secretion much more like that of the gland cells of animals than the more familiar method by a resinogenous layer of the cell wall as found in many trichomes.

In concluding, I wish to express my gratitude to Dr. R. A. Harper of Columbia University, under whose direction this work was carried out, for his helpful criticisms and suggestions.

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Explanation of plate 8

FIG. 1. Cell from a section of a very young stem of *Rhipsalis rhombea* showing cytoplasm about the periphery containing starch grains and nucleus. Magnification about 1,900 diameters.

FIG. 2. Cell adjoining that shown in FIG. 1, showing the first stage in the formation of a mucilage cell. Nucleus and nucleole are much enlarged, cell is filled with cytoplasm, no starch is present. Magnification about 1,900 diameters.

FIG. 3. Cell from a section of a young stem of *Rhipsalis rhombea.* A large nucleus and nucleole are present and the cytoplasm is spongy, as in FIG. 2. A narrow border of mucilage like a thin film lies between the cell wall and the cytoplasm. Magnification 1,300 diameters.

FIG. 4. Mucilage cell from the ovary wall of a bud of *Rhipsalis Houlletiana.* The cytoplasm is compressed to a small mass in the center of the cell, its organization lost, but the nucleus still persisting. Alveolar mucilage fills the space between the cell wall and the cytoplasm. Magnification 600 diameters.

FIG. 5. Mucilage cell from a flower bud of *Rhipsalis pachyptera.* The cytoplasm lies in the central part of the cell and is very much compressed. A few starch grains still persist, but nucleus and nucleole are disintegrated. Magnification 600 diameters.

FIG. 6. Section of a wall between a mucilage cell and two adjoining cells in a flower bud of *Rhipsalis pachyptera,* showing the middle lamella. Magnification 1,100 diameters.

FIG. 7. Photograph of a section from a flower bud of *Rhipsalis pachyptera* showing the zonation in a mucilage cell. The darker central portion is cytoplasm, the striations in the mucilage being nearly parallel to it.

A taxonomic study of Dumortiera*

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The genus *Dumortiera* was proposed in 1824 by Nees von Esenbeck for the reception of *Marchantia hirsuta* Sw. This species, which dates from 1788, was based on specimens from the mountains of Jamaica. Subsequent writers have assigned to it, however, a wide geographical distribution, its reputed range including most of the moist tropical and subtropical regions of the earth with extensions into certain temperate regions. According to the records the other species which have been referred to the genus are more restricted in their range, some of them having been reported from only one or two localities. These additions are not numerous, as the following complete list of species, arranged chronologically, will show:—

DUMORTIERA HIRSUTA (Sw.) Nees, 1824 (*Marchantia hirsuta* Sw., 1788);
D. SPATHYSII (Lindenb.) Nees, 1838 (*M. Spathysii* Lindenb., 1829);
D. IRRIGUA (Wils.) Nees, 1838 (*M. irrigua* Wils., 1833, *Hygropyla irrigua* Tayl., 1835);
D. NEPALENSIS (Tayl.) Nees, 1838 (*H. nepalensis* Tayl., 1836),
D. TRICHOCEPHALA (Hook.) Nees, 1838 (*Marchantia trichocephala* Hook., 1837);
D. DILATATA (Tayl.) Nees, 1847 (*Hygropyla dilatata* Tayl., 1844);
ASKEPOS BREVIPES Griff., 1849;
DUMORTIERA DENUDATA Mitt., 1861;
D. VELUTINA Schiffn., 1898;
D. CALCICOLA Campbell, 1918.

From this list three species may be at once excluded; they do not belong to *Dumortiera* and have already been transferred to their proper positions by writers. The species in question are: *D. Spathysii*, which is now regarded as a synonym of *Clevea Rousseliana* (Mont.) Leitg.; *D. dilatata*, a synonym of *Monoclea Forsteri* Hook.;† and *D. denudata*, the type species of the genus

* Contribution from the Osborn Botanical Laboratory.

† Leitgeb (7, p. 312) was the first to recognize that *H. dilatata* was a *Monoclea* and not a *Dumortiera*. He called it *M. dilatata*, supposing that it was distinct from *M. Forsteri*. His conclusions, unfortunately, were not based upon a study of the type material of *H. dilatata* but upon later New Zealand specimens, and his idea of *M. Forsteri* (in the opinion of Stephani) was gained from the American *M. Gottschei* Lindb., rather than from the true *M. Forsteri*. The type specimen of *H. dilatata* in the Taylor Herbarium shows conclusively that the species is a synonym of *M. Forsteri*.

Wiesnerella Schiffn. and now known as *W. denudata* (Mitt.) Steph. The remaining species have been the cause of much confusion from the taxonomic standpoint, and this is especially true of *D. hirsuta*, *D. irrigua*, *D. nepalensis* and *D. trichocephala*. To give some idea of this confusion it will be sufficient to quote from the writings of Schiffner and Stephani, two of the most prolific hepaticologists of Europe.

Schiffner, in 1893 (**9**, p. 36), estimated the number of species of *Dumortiera* as six, without enumerating them by name. He suggested, however, that they might all be forms of *D. hirsuta*, to which he attributed a range extending throughout all tropical countries. Under *D. hirsuta* he included the var. *irrigua*, a plant of Ireland, the Pyrenees, Italy and the southern United States. In another paper (**10**, p 275) published the same year, he listed the var. *irrigua* from Brazil. In 1899 (**11**, p. 387) he cited *D. hirsuta* somewhat doubtfully from Japan, the plants in question combining a densely papillose thallus with a bristly female receptacle. In 1900 (**12**, p. 25) he referred certain Javan specimens, which he had previously determined as *D. hirsuta*, to *D. trichocephala*, and stated that the true *D. hirsuta*, if it occurred in Java at all, must be much rarer than *D. hirsuta*. In 1902 (**13**, p. 274) he listed *D. irrigua*, this time as a species, from La Palma, one of the Canary Islands; and in 1909 (**15**, p. 482) he discussed the rhizoids of *D. irrigua* (in plants from Italy and Brazil) and of *D. hirsuta* (in plants from Java). He apparently now regards *D. irrigua* and *D. hirsuta* as distinct species and considers *D. trichocephala* a synonym of *D. hirsuta*.

Stephani's statements about the species in question leave an equally indefinite impression. In 1886 (**17**, p. 13; **18**, p. 94), he listed *D. hirsuta* from the African islands of San Thomé and Fernando Po; in 1888 (**19**, pp. 280, 300), from the West Indian islands of Hispaniola, Porto Rico and Dominica; in 1892 (**20**, p. 177), from Costa Rica; in 1895 (**22**, p. 304), from the African districts of Kamerun, Kilimanjaro and Usambara, and also from Queensland and northern New Zealand;* in 1897 (**23**, p. 78; **24**, p. 842), from Japan and the Hawaiian Islands. In 1894

* The New Zealand records seem to have been based on *D. dilatata* (see page 167, footnote); this species, for a time, was supposed to be a synonym of *D. hirsuta*.

(21, p. 6) he definitely recognized *D. irrigua* as a species, basing his observations on Italian material and emphasizing the impossibility of uniting it with *D. hirsuta*, and in 1897 (23, p. 78) he listed *D. irrigua* from Japan. In the same year (24, p. 842) he listed both *D. nepalensis* and *D. trichocephala* from the Hawaiian Islands. In his revision of *Dumortiera*, published in 1899 (25), he recognized the validity of *D. hirsuta* and *D. trichocephala* but included *D. nepalensis* and *D. irrigua* among the synonyms of *D. hirsuta*. This revision apparently represents his latest views. In it he restricted *D. trichocephala* to Asia and Oceanica, citing specimens from Tonkin, Birma, Java, Tahiti and Samoa, as well as from the Hawaiian Islands. He ascribed to *D. hirsuta* a much wider distribution, giving as localities many of those mentioned above and also the following: Mexico, Jamaica, Guadeloupe, Colombia and Brazil; Reunion; Nepal and Java; Tahiti; Ireland.

The divergent views of Schiffner and Stephani and the changes which these views have undergone are no more perplexing than some of the views advanced by other writers. They indicate that the characters distinguishing *D. hirsuta*, *D. irrigua*, *D. nepalensis* and *D. trichocephala* must be either untrustworthy or difficult to apply. The characters upon which *Askepos brevipes*, *Dumortiera velutina* and *D. calcicola* are based are likewise less satisfactory than might be desired and arouse the suspicion that variable and inconstant peculiarities have been too strongly emphasized. At the same time, as will be shown below, definite evidence has been presented that certain differential features may be transmitted from one generation to another, but whether these features are specific in value or merely indicative of varietal or racial differences is exceedingly difficult to determine. Even if they are regarded as specific, it must be admitted that the species of *Dumortiera* are much less clearly defined than those of most genera of the Marchantiaceae; they are little more than "small species," as this term is now employed in the literature of the bryophytes.

The characters most emphasized by writers, in distinguishing the various species of *Dumortiera*, have been drawn from the size and method of branching of the thallus; from the structural features of its upper surface; from the structure and configuration

of the receptacles; and from the size of the spores. These characters may be taken up in order.

In its general aspects the thallus presents great uniformity. It consists of a flat, strap-shaped structure, with more or less undulate margins, and clings loosely to the substratum. According to Ernst (4, p. 163; *pl. 18, f. 1, 2; pl. 20, f. 18, 19*) the marginal undulations tend to be more pronounced in *D. trichocephala* than in *D. velutina* and are often accompanied by irregular indentations, but these vague differences are neither constant nor of great significance. The differences in size which have been described seem likewise very uncertain, although Campbell, (2, p. 331) in his account of *D. calcicola* emphasizes the narrow thallus, measuring barely 5 mm. in width. Quoting again from Ernst (4, p. 162) *D. trichocephala* includes larger forms on the whole than *D. velutina*, the thallus attaining a maximum width of 3 cm., but it includes also forms which are no wider than those of *D. velutina*. The size seems to be very strongly influenced by external conditions.

The branching of the thallus is usually dichotomous but sometimes ventral. The sexual receptacles are terminal, the branches bearing them being variable in length and normally limited in growth. Not infrequently, however, a sexual branch innovates at the apex, the innovation growing in the same direction as the branch and broadening out from a stalk-like base. Such an innovation is usually found in connection with a male receptacle or a female receptacle which has failed to be fertilized; but even a sterile branch, the growth of which has been arrested in some way, is sometimes induced to innovate. Apical innovations in *Dumortiera* have commonly been regarded as somewhat abnormal, caused perhaps by unfavorable environmental conditions. In *D. calcicola*, where they occur more regularly, at least on sexual individuals, they give rise to jointed sympodial systems of very striking appearance and have been emphasized by Campbell (2, p. 334) as a specific peculiarity. Unfortunately similar sympodia have been recorded by Schiffner (10, p. 275) in specimens of "*D. hirsuta*" from New Guinea and by Ernst (4, p. 161) in specimens of *D. velutina* from Java, so that they are by no means confined to *D. calcicola*.

In its histological features the thallus differs strikingly from most of the other genera of the Marchantiaceae, since it lacks, either partially or completely, the usual dorsal epidermis and system of air-chambers. The simplification in structure which is thus exhibited is regarded as a derived condition, associated in some way with the usual moist and shaded habitat of the plants. By the earlier writers air chambers were supposed to be invariably absent. Taylor, indeed, in his account of *Hygropyla irrigua* (**26**, p. 391), described a system of branched and anastomosing lines (*rami*) on the upper surface of the thallus but did not intimate that there was any connection between these lines and chambers. Many years later Leitgeb (**7**, p. 308), working mainly on Taylor's species, confirmed his observations and showed that the lines were ridges, representing the boundary-walls of vestigial air chambers. In the vicinity of the apex he was able to demonstrate a short-lived epidermis with distorted pores and he noted that epidermal fragments or isolated cells sometimes persisted for a while on the boundary walls of older chambers. Close to the receptacles he observed the frequent occurrence of elongated papilliform cells in the spaces enclosed by the boundaries and pointed out the homology between these and the green cell-chains filling the air chambers of *Marchantia*.

In the forms which Leitgeb studied these papilliform cells seem to have been restricted to the vicinity of the receptacles. At any rate he made no mention of them in other parts of the thallus, and the figures which he afterwards published (**8**, *pl. 8, f. 8–11*) show a smooth superficial layer of cells. A few years later Spruce (**16**, p. 566) gave a detailed account of "*D. hirsuta*," based primarily on South American material and apparently found a very different state of affairs. According to his description the superficial cells are "papilloso-prominulae" and give the living plants a velvety appearance. If there were exceptions to this condition in any of his plants he did not allude to them. Goebel (**5**, p. 224, *f. 63*) described the surface of "*D. hirsuta*" in much the same way and figured the papilliform cells very clearly. Unfortunately he did not state the source of his material. He contrasted the species with an unnamed form from Ceylon, in which he found vestigial chambers but no surface papillae, this

form thus agreeing essentially with *D. irrigua*, as described by Leitgeb. Soon afterwards Campbell (1, p. 49), in specimens of "*D. trichocephala*," from the Hawaiian Islands, found neither papilliform cells nor vestigial chambers.

The descriptions of Leitgeb, Spruce, Goebel and Campbell thus record the following three types of surface in *Dumortiera:* (1) with both vestigial chambers and papilliform cells; (2) with vestigial chambers but without papilliform cells; (3) with neither vestigial chambers nor papilliform cells. When these types are clearly defined, as they sometimes are, they seem to yield excellent characters for the separation of species, although writers have expressed dissenting views regarding their value. Schiffner, for example, in his description of *D. velutina* (12, p. 26), emphasized the crowded papilliform cells as one of the features of the species, while Stephani claimed that such cells were present in all the species and that their persistence in *D. velutina* merely indicated a shaded environment. Coker (3, p. 226) explained the presence or absence of vestigial chambers in much the same way. In the vicinity of Chapel Hill, North Carolina, he found that plants of *D. hirsuta* growing in shaded, rather dry localities showed such chambers clearly, while plants in more exposed, wet localities were perfectly smooth; and he attributed these differences to environmental factors. Schiffner (14) criticized the views of Stephani and Coker. He maintained that the degree of development which the air chambers exhibited was not directly caused by the environment but that it depended upon inherited qualities. To support his statements he showed that "*D. trichocephala*" (with greatly reduced chambers) and *D. velutina* (with better-developed chambers and papilliform cells), often grew under exactly the same conditions in the primeval forests of Java and Sumatra and that both maintained their distinctive peculiarities. He showed further that plants of *D. velutina* from an almost dark well were exactly the same as those from sunny paths. His most convincing arguments, however, were drawn from plants which had been cultivated under identical conditions for about twenty years in the botanical garden at Prague. These plants represented *D. velutina* and *D. irrigua*, and their distinctive differences persisted unchanged.

Some of Goebel's recent observations (6, p. 628, 629) help to confirm Schiffner's deductions. He described a Brazilian *Dumortiera*, presumably a form of *D. hirsuta*, which lacked vestigial air chambers completely and found that none were formed even when the plants were cultivated under the same conditions as *D. velutina*, which developed its normal chambers and papilliform cells. He called attention to the fact that very young plants of *Marchantia* lack air chambers and he therefore interpreted the *Dumortiera* without chambers as a juvenile condition. In case air chambers are never formed there is simply, in his opinion, a persistence of the juvenile state. If air chambers are formed the presence or absence of papilliform cells indicates a greater or less advance beyond the condition without air chambers. In other words there are certain races or varieties or "species" of *Dumortiera* which are never able, even under the most advantageous of conditions, to advance beyond the state without air chambers, while other "species" can advance to various stages beyond this state. Goebel mentioned also a plant of "*D. hirsuta*," which gave rise to an adventive branch without chambers. Since "*D. hirsuta*," in his conception of the species, normally develops chambers, this branch was interpreted as a reversion to a juvenile state.

According to the writer's experience, although the three types of thallus are often distinctly marked, they are by no means invariably so. Even an individual thallus may sometimes bear crowded papilliform cells in an older portion and be smooth or nearly so nearer the apex; another may form vestigial air chambers for a while and then continue its growth without them. Such cases are further examples of reversions and indicate that these may be induced without the intervention of adventive outgrowths. The power to revert, which more or less advanced types thus clearly possess, complicates still further the conditions found in the genus and adds to the difficulty of defining specific limitations. If a form with crowded papillae represents a "species," a smooth form growing in the same area may represent merely a juvenile condition of the same thing or it may represent a "species" which can not advance. At the same time it must be admitted that smooth or nearly smooth states are the only ones which

occur over extensive areas, according to the information at hand. In Europe and Africa, for example, no forms with crowded papilliform cells have as yet been reported, although some of the plants have vestigial chambers while others have none. In such areas, therefore, the difficulties of distinguishing between forms with crowded papillae and smooth forms are eliminated, although the difficulties of distinguishing between forms with air chambers and those without them still remain. In the writer's opinion the latter distinction is less significant than the former, and it seems inexpedient at the present time to attempt to use it in the delimitation of species.

The receptacles of *Dumortiera*, which represent stalked branch-systems, have been repeatedly described (see, for example, Ernst, 4, pp. 173–178). The stalk of the male receptacle is extremely short but shows two rhizoid-furrows, agreeing in this respect with the much longer stalk of the female receptacle. The disc of the male receptacle is not clearly lobed and the antheridia are not arranged in radiating rows, although they clearly arise in acropetal succession. The disc of the female receptacle develops normally from eight to sixteen groups of archegonia on its lower surface. When the receptacle is young there are no distinct marginal lobes, but these become evident later on in case fertilization has taken place, the groups of archegonia being situated beneath the lobes. The involucre is thick and fleshy and shows a small apical opening; on its surface it bears scattered bristles. Similar bristles, which have been interpreted as modified rhizoids, occur on the upper surface of the disc, sometimes abundantly and sometimes sparingly, sometimes restricted to the marginal portions and sometimes more evenly distributed. Vestigial air chambers are not developed, and the surface-cells, although sometimes more or less convex, do not form papilliform outgrowths, even when the vegetative thallus forms them abundantly.

The features used in separating species have been drawn mainly from the female receptacle and relate more especially to the marginal lobes and the number and distribution of the dorsal bristles. According to Stephani (25) the receptacle of *D. trichocephala* is strongly convex and very bristly, while that of *D. hirsuta* is less convex, with the bristles confined to the marginal portions. He

describes further certain ridges or rays on the dorsal surface alternating with the lobes; these ridges branch by forking, the branches extending along the margins of the lobes. In *D. trichocephala* the branches are not connected in any way and thus leave sharp sinuses between the lobes; in *D. hirsuta* the branches are connected by thallus-substance, and the sinuses thus appear lunulate. These distinctions would be very helpful if they were at all constant but, in the writer's experience, this is not the case. All gradations occur between strongly bristly receptacles and those with marginal bristles only, while the ridges with their branches, although sometimes fairly distinct, are often vague and evanescent. Neither is there any correspondence between differences in the thallus and differences in the female receptacle. A smooth or nearly smooth form, for example, may bear receptacles with many bristles scattered over the surface or with only a few bristles restricted to the margin.

The characters assigned to the female receptacle of *D. velutina* seem at first sight to be more trustworthy. According to Schiffner (**12**, p. 26) the disc is depressed-conical with broad lobes and very shallow sinuses, the upper surface bearing few or no bristles. The figures published by Ernst (**4**, *pl. 18, f. 1*) and by Campbell (**2**, *text-f. 3*) represent the upper surface as perfectly smooth, but otherwise agree with Schiffner's description. In material of *D. velutina* from Java, determined by Campbell, the receptacles agree closely with his figures and show no bristles. This is not the case, unfortunately, with the specimens distributed by Schiffner in his Iter Indicum, one of which came from Java (No. 27) and the other from Sumatra (No. 32). In these the immature receptacles are more or less bristly and some of the bristles are scattered over the upper surface. The older receptacles tend to be less bristly, but their marginal sinuses are often deeper than Schiffner's description and the published figures indicate. It would thus appear that the characters assigned to the female receptacle by Schiffner were subject to variation and therefore untrustworthy.

Although the antheridia and archegonia are usually borne on separate receptacles in *Dumortiera*, bisexual receptacles have long been known. They were first described by Taylor (**26**, p. 391)

in *D. irrigua*, where they seem to be somewhat of a rarity. Ernst, however, demonstrated their frequency in Javan specimens of "*D. trichocephala*" (4, p. 207). He found them also in *D. velutina* but much more rarely and associated this difference with the prevailingly monoicous inflorescence of "*D. trichocephala*" and the prevailingly dioicous inflorescence of *D. velutina*. Whether or not bisexual receptacles are frequent in American forms of *Dumortiera* remains to be determined.

The spores of *Dumortiera* vary in color from pale to dark brown. The tetrahedral form persists until maturity, although the ridges separating the faces are sometimes difficult to distinguish. The surface-markings are remarkably uniform. Each face bears a series of minute and crowded papillae or short lamellae, which are usually irregularly distributed but which sometimes show a slight tendency to be arranged in short rows. No reticulum is developed. With respect to size statements in the literature are not in accordance. Stephani (25) gives a diameter of 25 μ for *D. trichocephala* and of 34 μ for *D. hirsuta*; for *D. velutina* he gives no measurements. Ernst's figures are considerably higher (4, p. 178); he gives a length of 45–60 μ and a width of 35–50 μ, without distinguishing between *D. trichocephala* and *D. velutina*. Campbell (2, p. 329) states that the spores of *D. trichocephala* are about 20 μ long while those of *D. velutina* are about 29 μ. The writer has examined spores of various forms from widely separated stations and finds that the long diameter measures 20–30 μ, a considerable range being often present in a single capsule. Apparently little help can be obtained from the spores in the separation of species.

The preceding discussion brings out the untrustworthy nature and inconstancy of certain differential characters which have been employed in defining the species of *Dumortiera*. Those drawn from the size and method of branching of the thallus seem especially unreliable. Those drawn from the female receptacle and the spores are scarcely more satisfactory. On the basis of characters drawn from the structural features of the vegetative thallus, the two following species may be distinguished, and these are the only ones which the writer would recognize at the present time:

Upper surface of thallus smooth or nearly so throughout (although often showing vestigial air chambers). 1. *D. hirsuta.*
Upper surface of thallus with crowded papilliform cells, at least in certain portions (always showing vestigial air chambers). 2. *D. nepalensis.*

1. DUMORTIERA HIRSUTA (Sw.) Nees

Marchantia hirsuta Sw. Prodr. Fl. Ind. Occid. 145. 1788.
Dumortiera hirsuta Nees, Nova Acta Acad. Leop.-Carol. **12**: 410. 1824.
Marchantia irrigua Wils.; Hooker, Brit. Fl. **2**: 106. 1833.
Hygropyla irrigua Tayl.; Mackay, Fl. Hibern. **2**: 54. 1836.
Dumortiera irrigua Nees, Naturg. Europ. Leberm. **4**: 159. 1838.
?*Dumortiera hirsuta angustior* G. L. & N. Syn. Hep. 544. 1846.
?*Dumortiera hirsuta intermedia* G. L. & N. *l. c.*
?*Askepos brevipes* Griffith, Not. Pl. Asiat. **2**: 340. 1849.
Dumortiera hirsuta irrigua Spruce, Trans. Bot. Soc. Edinb. **15**: 566. 1885.

It seems unnecessary to give a list of the many specimens which the writer has referred to *D. hirsuta.* They represent a very extensive geographical range, for the most part tropical, and include a few sterile and poorly developed plants, which are not altogether above suspicion. This is especially the case when such plants were found in regions where *D. nepalensis* also occurs. The specimens examined came from the following states, countries, and islands: Pennsylvania, North Carolina, South Carolina, Kentucky, Tennessee, Georgia, Florida, Alabama, Missouri, and Arkansas; Mexico, Guatemala, Nicaragua and Panama; Bermuda; Cuba, Hispaniola, Jamaica, Porto Rico, Montserrat, Guadeloupe, Martinique and Grenada; Colombia, Peru and Bolivia; Venezuela, Brazil and Paraguay; Ireland, England (East Sussex) and France (Hautes-Pyrénées); Madeira and the Canary Islands; Fernando Po and Kamerun; China, India (including Nepal and Ceylon), French Indo-China and Japan; the Philippine Islands, Java and the Hawaiian Islands.

It has unfortunately been impossible to secure the actual type specimen of *Marchantia hirsuta* for examination. The specific name "*hirsuta*" is here associated with the form without surface papillae, because a Swartzian specimen in the British Museum (kindly examined by Mr. Gepp) is smooth and because the

smooth form predominates in the West Indies. Out of over fifty West Indian specimens examined (including fifteen from Jamaica, the type-locality for *M. hirsuta*) only two showed papillae. Of course this evidence is not absolutely conclusive, and if it should ever be proved that the original specimen of *M. hirsuta* represented the papillose form, the synonymy of the species would have to be revised.

There is no such doubt about *Marchantia irrigua*. The Irish specimens of *Dumortiera* are all smooth on the upper surface, with rather vague vestiges of air chambers, and (as Schiffner has shown) never produce papillae even under cultivation. The vars. *angustior* and *intermedia* of the Synopsis need further study. Var. *angustior* was based on Mexican plants with a strongly setulose female receptacle, while var. *intermedia* was based on plants from Peru and South Africa with fewer bristles on the receptacle. Neither of these varieties is known to the writer from authentic material. The same thing is true of Griffith's *Askepos brevipes*, which was based on Indian specimens. Schiffner reduced Griffith's genus to synonymy under *Dumortiera* in 1893 (**9**, p. 35) but has apparently made no definite reference to its single species. According to Griffith's description and figures *A. brevipes* is clearly a *Dumortiera*. It is here referred to *D. hirsuta*, rather than to *D. nepalensis*, on the basis of one of Griffith's specimens in the Mitten Herbarium. This specimen came from Dehra, India, and is labelled "*Askepos*"; the thallus shows a smooth dorsal surface with vestigial air chambers, and the female receptacle bears scattered bristles.

2. DUMORTIERA NEPALENSIS (Tayl.) Nees

Hygropyla nepalensis Tayl. Trans. Linn. Soc. **17**: 392. *pl. 15, f. 2.* 1836.

Marchantia trichocephala Hook. Icon. Pl. *pl. 158.* 1837.

Dumortiera nepalensis Nees, Naturg. Europ. Leberm. **4**: 169. 1838.

Dumortiera trichocephala Nees, *l. c.* **4**: 499. 1838.

Dumortiera hirsuta latior G. L. & N. Syn. Hep. 544. 1846.

Dumortiera hirsuta trichopus Spruce, Trans. Bot. Soc. Edinb. **15**: 567. 1885.

Dumortiera velutina Schiffn. Denkschr. Math.-Naturw. Cl. Kais. Acad. Wiss. Wien **67**: 156. 1899.

Dumortiera calcicola Campbell, Ann. Bot. **32**: 334. *pl. 8 + f. 9.* 1918.

According to the knowledge at hand the range of *D. nepalensis* includes neither Europe nor Africa; otherwise it corresponds pretty closely with that of *D. hirsuta.* In certain parts of its range, such as the southern United States and the West Indies, it has been rarely collected; in other parts of its range, such as southeastern Asia, it seems to be more abundant. The following specimens have been examined:—

GEORGIA: Forest Falls, Decatur County, 1901, *R. M. Harper 1193a* (apparently mixed with *D. hirsuta*).

FLORIDA: Gainesville and vicinity, 1909, *R. M. Harper 13;* 1915, *N. L. T. Nelson 100;* Pineola, 1918, *J. K. Small.*

MEXICO: Honey, Puebla, 1908, *Barnes & Land 520, 526;* Jalapa, Vera Cruz, 1908, *Barnes & Land 564.*

HONDURAS: trail near Rio Platano, 1903, *P. Wilson 682.*

JAMAICA: near Newhaven Gap, 1906, *A. W. Evans 604.*

PORTO RICO: between Adjuntas and Ponce, 1906, *M. A. Howe 1256.*

COLOMBIA: Bogotá, *W. Weir.*

ECUADOR: near Baños, *R. Spruce* (distributed as *D. hirsuta* var. in Hep. Spruceanae).

PERU: Monte Guayrapurina, *R. Spruce* (distributed as *D. hirsuta* var. *trichopus* in Hep. Spruceanae).

VENEZUELA: near Caracas, 1854, *Burchel;* valley of the Rio Limon, Aragua, 1913, *H. Pittier 6070*

CHINA: Hongkong, collector unknown.

INDIA: Nepal, 1820, *N. Wallich* (type of *Hygropyla nepalensis*); Sikkim-Himalaya, 1889, *Fathers Decoby & Schaul 321* (determined by Schiffner as *D. velutina*).

FEDERATED MALAY STATES: Taiping Hills, 1912, *D. H. Campbell.*

JAPAN: Uzen, 1888, *M. Miyoshi 4;* Tokio, 1898, *K. Miyake 1;* Kioto, *G. Shimadzu & Co. 12.*

PHILIPPINE ISLANDS: Mt. Banjao, Tayabas Province, Luzon, 1907, *F. W. Foxworthy 2305;* Benguet Subprovince, Luzon, 1901,

E. D. Merrill 7901; 1910, *E. Fénix 12814;* 1907, *A. D. A. Elmer 8614;* Bontoc Subprovince, Luzon, 1910, *Father Vanoverbergh 875;* near the Shibuyan River, Davao District, Mindanao, 1904, *E. B. Copeland 985.*

SUMATRA: foot of Mt. Singalang, 1894, *V. Schiffner* (distributed as *D. velutina* in Iter Ind. *32*).

JAVA: Buitenzorg, *F. A. W. Miquel;* same locality, 1894, *V. Schiffner* (distributed as *D. velutina* in Iter Ind. *27*); same locality, 1906, *D. H. Campbell;* Tjibodas, Preanger Province, 1894, *V. Schiffner* (distributed as *D. hirsuta* var. *latior* in Iter Ind. *24*).

BORNEO: Bidi Caves, Bau, Sarawak, 1913, *D. H. Campbell* (type of *D. calcicola*).

HAWAIIAN ISLANDS: without definite localities, *D. Douglas 71* (type of *Marchantia trichocephala*); 1864–70, *H. N. Bolander;* 1876, *J. Bailey 1;* Honolulu, Oahu, 1892, *D. H. Campbell;* Panoa, Oahu, 1895, *A. A. Heller 2330;* Manoa Valley, Oahu, 1917, *D. H. Campbell;* Oahu, 1918, *H. L. Lyon;* West Maui, 1875, *D. D. Baldwin.*

SAMOAN ISLANDS: Utumapa, Upolu, *C. & L. Rechinger* (distributed as *D. velutina* in Krypt Exsic. Mus. Palat. Vindob. *1391*); without definite locality, 1888, *Frances C. Prince.*

The type specimen of *Hygropyla nepalensis* in the Taylor Herbarium shows a thallus with numerous surface papillae associated, as Taylor's figures indicate, with a bristly female receptacle. The type specimen of *Marchantia trichocephala* in the same herbarium shows a thallus with still more numerous papillae and female receptacles which are still more bristly. Both specimens clearly belong to the same specific type. The var. *latior* of *D. hirsuta,* which is listed above in the synonymy, was probably an admixture; it was based on specimens from various parts of the world and may have included forms which would now be referred to the true *D. hirsuta.* The var. *trichopus,* however, is undoubtedly a true synonym of *D. nepalensis,* as the specimens distributed by Spruce clearly indicate.

The last two species which are listed among the synonyms have already been discussed to some extent in the preceding pages. *D. velutina* is distinguished from strongly papillose forms of *D. nepalensis* by certain features of the female receptacle, but

these features (according to the evidence at hand) are too inconstant to be considered of specific value. In *D. calcicola*, as already pointed out, the characters drawn from the size of the thallus and from the sympodia developed by the sexual plants are of little significance. The characters drawn from the immature female receptacles with unfertilized archegonia and from the male receptacles are likewise of doubtful value. Unfortunately the papilliform cells of the thallus are rather scantily developed in the type material, but this condition is often duplicated in undoubted *D. nepalensis*.

For valuable assistance in the preparation of this paper the writer would express his thanks to Professor W. G. Farlow, Professor D. H. Campbell, Dr. Marshall A. Howe and Miss Caroline C. Haynes. Through their generosity it has been possible to study the types of *D. irrigua*, *D. nepalensis*, *D. trichocephala*, *D. dilatata* and *D. calcicola*, as well as other interesting and authentic material.

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Notes on plants of the southern United States—V

FRANCIS W. PENNELL

KALMIELLA HIRSUTA (Walt.) Small

Sandy scrub-land, between Theodore and Hollanders Island, Mobile County, Alabama, September 3, 1912, *Pennell 4513*.

POLYPODIUM FLORIBUNDUM (Nutt.) Greene

Open pine-land, Biloxi, Harrison County, Mississippi, August 28, 1912, *Pennell 4405*.

SABATIA ELLIOTTII Steud.

Moist scrub-land, between Theodore and Hollanders Island, September 3, 1912, *Pennell 4512*.

Dasystephana tenuifolia (Raf.) Pennell, comb. nov.

Diploma tenuifolia Raf. Fl. Tell. **3**: 27. 1837. "Florida . . . seen in the herb. of Torrey." The type, labeled in Rafinesque's handwriting "G. tenufolia Raf. Monog.," is in the Columbia University Herbarium at the New York Botanical Garden. It bears data of collection, "Florida, Mr. Croom, 1832, flowers white."

In the American Journal of Science for October, 1833 (**25**: 69), H. B. Croom records "Gentiana alba (White flowered Gentian)" as growing in "wet pine woods" in Middle Florida, a region defined as "that tract of country which lies between the Suwanee River on the east, and the Apalachicola on the west." His "observations were chiefly made . . . about twenty miles west of Tallahassee, about thirty miles from the Gulf of Mexico, in latitude about 30° 30′." The plant was seen in bloom January 1–5, 1833, and must certainly be the same species as the plant sent Dr. Torrey.

Dasystephana tenuifolia is most nearly allied to *D. Porphyrio* (Gmel.) Small, long known as *Gentiana angustifolia* Michx. Rafinesque briefly distinguishes the two by certain features, the

most obvious of which is the white corolla of the southern plant. Southern botanical authors treating of the Carolina flora, describe the blue-flowered species, but Chapman, working on the Gulf coast, knew only the white-blooming low-growing plant. A brief contrast of the two would be:

Plant 3–5 dm. tall. Corolla deep-blue within. Stamens and pistil about equaling the tube of the corolla. Stigmas spreading, 3–4 mm. long. Sandy pine-lands, New Jersey to South Carolina. 1. *D. Porphyrio.*

Plant 1–2.5 dm. tall. Corolla white within. Stamens and pistil only about one half the length of the corolla-tube. Stigmas slightly spreading, about 1 mm. long. Low pine barrens, West Florida. 2. *D. tenuifolia.*

Beside the type nearly all the specimens of *D. tenuifolia* seen are from the Chapman Herbarium, and his No. 467b, collected November 2, 1884, and distributed by the Biltmore Herbarium, may be cited. The only specimens of recent collecting which have come to my notice were obtained by Dr. G. C. Fisher at Red Bay, Walter County, Florida, in January, 1917. The same observer has found the plant at Sanborn in Wakulla County. These definite localities enable us to predict the occurrence of the species throughout the low moist pine-lands between Apalachee Bay and Escambia Bay.

Acerates hirtella Pennell, sp. nov.

? *Oligoron longifolium hirsutum* Raf. New Fl. Am. 4: 60. 1838. No locality given, but description of pedicels as long-hirsute suggests, though it over-emphasizes, a feature of the plant here considered.

Stem 6–10 dm. tall, stout, strongly puberulent in lines above. Leaves scattered, numerous, rather crowded, lanceolate-linear, 9–17 cm. long, 0.6–1.4 cm. wide, scabro-puberulent above and on the veins beneath. Peduncles stout, less than 3 cm. long, scabro-hirtellous. Umbels four to twelve, twenty-five to one hundred flowered. Pedicels 12–15 mm. long, hirtellous with spreading hairs. Flowers 8–8.5 mm. long. Sepals 2 mm. long, lanceolate-acuminate, hirtellous on the back. Petals 5 mm. long, lanceolate, greenish yellow, sometimes slightly purple-tinged on back toward apex, crenulate at apex. Column 0.5–0.7 mm. long. Hoods entire, rounded, one half to two thirds the length of the anthers. Anthers acute, each with two wings which are angled above the

middle. Follicles erect on reflexed fruiting pedicels, 10 cm. long, lanceolate, short-caudate, hirtellous-pubescent. Seeds obovoid, flat, 8 mm. long. Coma silvery, 35 mm. long.

TYPE: dry soil, east of Carthage, Jasper County, Missouri, *F. W. Pennell 5372*, in the herbarium of the University of Pennsylvania.

Wet to dry prairies, northern Illinois to eastern Kansas, and in "swamps" in Michigan. Probably extends to Oklahoma, as Nuttall collected it on the "Red River." This is the plant of the Mississippi Valley which has been merged with the Coastal Plain *A. floridana* (Lam.) A. S. Hitchc., and the following numbers are characteristic, *H. S. Reynolds 28*, *Agnes Chase 1439*, *J. R. Gardner 563*, *B. F. Bush 244*, *A. S. Hitchcock 763*.

The key below contrasts these two species:

Puberulence finely cinereous. Pedicels finely puberulent with incurved hairs. Hoods two thirds to three fourths the length of the anthers. Seeds 9-10 mm. long, dark-brown. Leaves not crowded, narrowly to broadly linear, glabrate. Flowers 7 mm. long. Petals strongly purple externally toward apex, with a narrow white border. Umbels one to six, ten to thirty-flowered, on peduncles reaching 3–9 cm. long. Capsule about 11 cm. long, narrowly lanceolate, long-caudate, finely appressed-puberulent. 1. *A. floridana.*

Puberulence more densely cinereous. Pedicels pubescent with spreading hairs. Hoods one half to two thirds the length of the anthers. Seeds 8 mm. long, cinnamon. Leaves crowded, broadly linear, scabrous to the touch. Flowers 8-8.5 mm. long. Petals greenish, sometimes slightly greenish externally toward apex, with a broader white border. Umbels four to twelve, twenty-five- to one hundred-flowered, on peduncles not over 3 cm. long. Capsule lanceolate, short-caudate, 10 cm. long, hirtellous-pubescent. 2. *A. hirtella.*

EVOLVULUS SERICEUS Sw.

Two forms were collected together on black calcareous soil, Edwards Plateau, northwest of New Braunfels, Comal County, Texas, September 14, 1913, *Pennell 5440, 5442*. No. 5440, with broader densely white-lanate leaves, bore blue corollas; No. 5442, with narrower leaves, strigose-lanate beneath, bore pale blue corollas. The latter is nearer the typical form of the West Indies.

PHLOX FLORIDANA Benth.

Dry sandy pine-land, east of Mississippi City, Harrison County, Mississippi, August 27, 1912, *Pennell 4353*.

EUPLOCA RACEMOSA Rose & Standley

Dry sandy oak-land, west of Sheridan, Colorado County, Texas, September 21, 1913, *Pennell 5516*. This agrees closely with the description of the species of western Texas. It is probably most readily distinguished from *E. convolvulacea* Nutt. by its narrower leaves, lanceolate or nearly so in the specimens seen. Other Texan collections to be referred here are: San Antonio, *E. Palmer 889;* western Texas, *S. B. Buckley*.

VERBENA VENOSA Gill. & Hook.

Moist soil, Mandeville, St. Tammany Parish, Louisiana, August 15, 1912, *Pennell 4204;* moist soil, Catalpa, West Feliciana Parish, August 24, 1912, *Pennell 4332*. Introduced from South America; reported from Houston, Texas, and previously collected in Louisiana in Plaquemines Parish, *A. B. Langlois 49*.

MONARDA PUNCTATA L.

The species is widespread and abundant through most of the Coastal Plain of the southeastern states, occurring inland in the southern Appalachians and westward to Sapulpa, Creek County, Oklahoma, *Pennell 5390*. Two geographical subspecies, which seem worthy of recognition, may be distinguished from the typical form of the species and from each other by the following key:

Leaves lanceolate to ovate-lanceolate, their blades obviously wider proximally and with definite petioles. Corolla conspicuously spotted.	
Stem finely appressed-pubescent.	1. *M. punctata*.
Stem pubescent with spreading hairs.	1a. *M. punctata villicaulis*
Leaves linear-lanceolate, obscurely petioled. Corolla not or scarcely spotted.	1b. *M. punctata immaculata*.

1a. **Monarda punctata villicaulis** Pennell, subsp. nov.

Stem pubescent with spreading hairs. Plant usually stouter than in the typical form.

TYPE: dry sandy open soil, Clarke, Lake County, Indiana, collected in flower August 22, 1915, *F. W. Pennell 6412;* in the herbarium of the New York Botanical Garden.

Sandy soil, northern Indiana and northern Illinois; far isolated from the typical species of the Coastal Plain. Other collections seen are:

INDIANA. Kosciusko: Winona, *C. C. Deam 1494;* Lake: Whitings, *N. L. Britton.*

ILLINOIS. Cook: Hyde Park, *A. Chase 1166* (sand near lake); Pullman (Y).

1*b*. **Monarda punctata immaculata** Pennell, subsp. nov.

Stem pubescent with fine reflexed appressed hairs. Leaves linear-lanceolate, obscurely petioled. Corolla not or scarcely spotted.

TYPE: sandy soil, Aloe, Victoria County, Texas, collected in flower September 8, 1913, *F. W Pennell 5494;* in the herbarium of the University of Pennsylvania; iso-type in the herbarium of the New York Botanical Garden.

Also seen from Texas, without locality, collected by Charles Wright.

CLINOPODIUM COCCINEUM (Nutt.) Kuntze

Dry sandy pine-land, Biloxi, Harrison County, Mississippi, August 27, 1912, *Pennell 4372;* also Mississippi City, Harrison County, *Pennell 4355.*

Dry sandy ridges in the longleaf pine-land, southern Georgia and northern Florida to southern Mississippi.

NEW YORK BOTANICAL GARDEN.

INDEX TO AMERICAN BOTANICAL LITERATURE

1905–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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New and old species of Opuntia

DAVID GRIFFITHS

(WITH PLATES 9 AND 10)

It is desirable again to record a few facts resulting from our culture of species of *Opuntia* upon the Department of Agriculture grounds at Chico, California. The species here discussed have been under observation a long time. Eight are here described for the first time and two are recognized for the first time since originally described.

Opuntia effulgia sp. nov.

A glistening, dark green, compactly-branched, stocky, turgid species of the tree type, with heavy trunk and having a rounded bowl, height 1.5-2 m. with us now at six years of age, and having a spread of branch of about 2 m.; joints subcircular to broadly obovate, about 18 x 28 cm. thick, glossy, slightly raised at areoles and having a lighter indefinite spot on the tubercle below the areoles, finally becoming smooth surfaced; areoles at first brown with prominent wool, 2–3 mm. in diameter, enlarging in age to 5 mm. or more and becoming gray; spicules scarcely visible except on old trunks where they become 2–3 mm. long, in a compact tuft in upper part of areole, brown to light brown; spines few, short, white or mostly dirty gray, none to 1 or 2, 5-15 mm. long, small, straight, stout, flattened and curved on old trunks where they become stouter and a little longer, but never numerous; flowers yellow, small, 4 cm. in diameter, the petals nearly erect, turning pinkish late in the day, filaments at first greenish, style white, but both reddish-tinged in the afternoon; fruit subglobose, mostly

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deeply pitted or sunken, 5.5 x 7.5 cm., purplish, glossy dark red marked with irregular darker lines about areoles which are black with central tuft of brown spicules and one or more variegated, or brownish, fugacious spines 4 mm. long; rind thick, pulp light purplish-red and somewhat mottled, seeds small, dark, almost marginless, angular.

This species, characterized by its dark, glossy, bright green, bloomless, turgid, stocky aspect, and the nature of its fruits, might be referred to the spineless group. I am, however, not ready to associate it with any described botanical species, for in my opinion it is a spineless form of an undescribed spiny Mexican species whose limitations I am not yet familiar enough with. A few seedling generations would probably throw some light on its affinities, but I have not yet been able to grow them.

The type is my inventory No. 8040, secured at San Luis Potosi, Mexico, in August, 1905. It is commonly referred to as "nopal camueso" by the natives. It has been hardy at Chico, California, except during the freeze of 1913.

Opuntia cyanea sp. nov.

An erect, spreading, tree-like plant becoming 2–3 m. high at six years of age from cuttings and having a spread of about 3 m.; joints obovate, widest at upper third to fourth, slightly glaucous, decidedly blue-green, the last year's joints commonly 20 x 32 cm., but often larger and frequently very much smaller; areoles subcircular to ovate or even elliptical, 25–30 mm. apart on last year's joints, about 3 mm. long, brown, fading to a dirty gray; spicules straw-colored, not visible until second year and then only at base of joints where they continue to increase in a compact tuft 1 mm. or so in length for a year or more, but never becoming prominent; spines white, few, only an occasional one 1–1.5 cm. long in an occasional areole, turning to a dirty, semi-translucent condition, seldom increasing at all in age; flower buds dull, light greenish-red, short-conical pointed, flowers dull, light orange-red, developing more red as day advances and coloring still deeper after closing, often 7.5 cm. in diameter, filaments greenish, turning pink, style white, tinting a little toward close of day, stigma light green 10–12-parted, turning pinkish after closing; fruit light yellowish-white, palatable, rind of same color, pulp distinctly greenish even when fully ripe, subglobose to obovate, about 62 x 70 mm., with slightly concaved umbilicus, its areoles subcircular, 2.5 mm. in diameter, with prominent, tawny wool, and a central tuft of straw-colored spicules

projecting less than 1 mm. beyond wool, fugacious spines, few, brown to yellowish, 0.5–0.75 cm. long, mostly in upper areoles.

This species has come to us from various Mexican sources. I first secured it at Aguas Calientes, Mexico, in 1905; later at Mixcoac, Mexico. The type is established, however. upon plants grown from seed secured at Del Rio, Texas, July, 1908. The plants from which this seed was secured were brought originally from Mexico. The type is carried under my inventory No. 9410. One or possibly two other collections of it have been grown to maturity.

This is well characterized as a blue-green spineless (nearly) species with fruit pulp green and palatable. I have no suggestions regarding its spiny affinity at present.

Opuntia diversispina sp. nov.

Plants erect, tree-like, 1–1.5 m. high and with a similar spread, joints obovate, broadly rounded above, 14 x 25 cm., to broadest at middle, and pointed above and below and measuring 14 x 30 cm., dark, glossy green, but likely to be yellowish in exposed surfaces, slightly when at all raised at areoles the second year; areoles subcircular to broadly oval, 4 mm. in length, brown, turning dirty gray to black; spines on second season's growth 3 to 6, yellow, 12–15 mm. long or less, either porrect or sloping down on edges of joints the second year or late the first, becoming more recurved and increasing in number in age with a variable number, 20 to 30, spicule-like yellow bristles, 6–12 mm. long, scattered mainly through upper edge of areoles, widely spreading, and requiring careful examination to be distinguished from the spines, the lower portion of areole containing 2 to 4 white, delicate, wavy, bent and twisted hair-like bristles besides; spicules 1–2 mm. long in a compact tuft near upper edge of areole, but not appearing until late in the year or even not until the second year; flower buds dull red with segments closely appressed; flowers yellow, red exteriorly in portions of petals exposed in the bud, fading to a light pink late in the day, filaments greenish at base but mostly white, style white, stigma large, medium green, 8–9-parted, petals broadly rounded at apex, mucronate, becoming more or less laciniate late in the day; fruit subglobose to obovate about 22 x 30 mm., yellow or greenish, deeply pitted, its pulvini 2 mm. in diameter, tawny, bearing a profusion of flexuous, hair-like, weak, fugacious spines 10–12 mm. long. [PLATE 9.]

This species has been in our collection for many years. Its

origin is not known, but was grown from seed at our Brownsville station about 1910. The records regarding the origin of the packet of seed have been lost. It was sent us by some correspondent. It was hardy but difficult to grow out-of-doors at Brownsville, Texas, apparently on account of the excessive humidity, but we have been unable to grow it to fruitage in open ground at Chico, California, on account of low temperatures.

The description here written is from specimens grown in a sash house in which the sash is slipped into a permanent framework on the advent of cold weather in autumn and removed as soon as danger of hard freezes is over in the spring. This arrangement also protects the plants from the excessive winter rains of this locality. So far as spination is concerned this species is more closely related to *O. Scheeri* A. Weber than any other known to me. It fruits poorly with us at Chico, although there is always an abundant blossom. Most of the ovaries fall soon after anthesis and the few that remain seldom ripen into plump, normal fruits. Usually a half dozen fertile seed is the most we get from the few fruits that mature.

The type has been carried under our South Texas inventory No. 2836, ordinarily written S. T. G. 2836.

Opuntia hispanica sp. nov.

An erect to ascending, spreading, widely and almost divaricately branched species, 3 m. or more high, with about an equal spread, making a globular-topped tree or, when grown from cuttings and not trimmed, a large hemispherical shrub—a tree headed on the ground; joints 14–15 x 30–41 cm., narrow, obovate, long, gradually tapering below, bright dark green, edges more or less notched with the raised areoles but smooth after one year; areoles obovate, brown, becoming dirty black, 3 mm. long, enlarging in age to subcircular and 5 mm. in diameter; spicules not visible, yellow; spines very numerous, formidable, white with translucent tips, 2 to 6, mostly 3 or 4, porrect, diverging in all directions, flattened, twisted, not annular, the longer central 3–4 cm. and the others about 2 cm. with an occasional one only about 1 cm. long, increasing on old trunks to 10 or more and variously curved and bent, variable, some even 5 cm. long and porrect, when 4 usually 2 on same level in lower part of areole and the other two one above the other directly above and between the first two; buds blunt, short-pointed, dull dark greenish with only a little red, edges of

scales white, thin and almost fimbriate, flowers yellow, turning slightly orange late in the day, 5 cm. in diameter, filaments light yellow, style white or slightly tinted above, stigma very light green, conical, 8–10-parted; fruit large, pyriform, about 55 x 90 mm. with flat flower scar, greenish white, with large, subcircular, brown areoles, about 3 mm. in diameter, bearing a compact tuft of yellow spicules 1 mm. long in center and 1 to 5 delicate, fugacious spines below.

The species is known to me from a single number which was received from Senor Ambrosio Eschauzier, of Seville, Spain. It was received under the common name "Americanos." It is quite distinct from anything else which we have cultivated, particularly in its habit of growth, shape of its joints, and spination. In some of its vegetative characters it resembles most closely *O. gymnocarpa* A. Weber, but differs from that species in being exceedingly spiny in its branching habits and in color and general character of its fruit. The fruit has considerable similarity that to of *O. elongata* Haw., and the nature of the branching is also similar to that species. It is rapid of growth and new growth starts each year from just below the tip of the last joint, making a very open, awkward species to handle in the field on account of its widely spreading and even somewhat drooping habit of branching.

The species is quite hardy at Chico, California, having been only slightly injured during the severe freeze of 1913. The fruits are edible and belong to the "blanca" group of the Mexicans, in which the expressed juice is limpid with no solids in suspension.

The type is carried in our collection under Seed and Plant Introduction No. 15840, and was secured from Sr. Ambrosio Eschauzier, Seville, Spain, through the kindness of Sr. Francisco Eschauzier, San Luis Potosi, Mexico. There is little doubt that it is of Mexican origin, but it is known to me only from this inventory number.

Opuntia chata sp. nov.

An arborescent, compact, erect to ascending species 2–3 m. or more high and with an equivalent spread of branch; joints subcircular to broadly obovate 24 x 32 cm. or often only 18–20 cm. in diameter; glaucous, gray-green, slightly raised at areoles; areoles broadly obovate on sides of joints, more narrow on edges, brown, turning dirty black, 2–3 mm. long, becoming subcircular and

enlarged in age; spines white, short, porrect, diverging, at one year of age, about 1 cm. or less in length, straight, stiff, but not stout, all but lowermost areoles armed, very variable in number, averaging 2 to 5; mostly about 4, later increasing irregularly to 6 to 10 and in length to 2 cm.; spicules yellow in a compact tuft one mm. long in upper part of areole, at first surrounded by narrow zone of brown wool, but this soon crowded out by increased spicular growth, not becoming any more conspicuous in age; flowers yellow, rather undersized, inclined to be slightly greenish tinged within, seldom 5 cm. in diameter when fully open; fruit obovate about 45 x 58 mm. yellowish-white, bleaching towards spring to a dirty white, rind same color as epidermis, pulp purplish-red and difficult of separation from the thick rind.

The species is one of the stockiest and strongest growers we have in our plantation, but it is not rapid in its vegetative growth like some of the spineless forms. It is a striking species for many reasons. Its glaucous, gray-green color is attractive. Its fruits are medium sized, not edible raw, but are used cooked and pickled. It is remarkable from the fact that the fruits cling on the plants until the next season in its natural habitat, but with us in California there may be a few fruits holding over even to the third year. They never, however, like some other species become incorporated as a permanent part of the plant. It is a remarkable thing also that under our conditions we seldom, if ever, have perfect fruits upon the plants in the spring, they being more subject to injury from low temperatures than the plant itself. Consequently, it is the rule to find practically all the fruits injured slightly on one side by cold weather in the spring. They, however, appear to mature perfectly in autumn.

The type is preserved under my inventory No. 8086 and was collected originally at Aguas Calientes, Mexico, August, 1905. It has been grown by us successfully in the open at Brownsville, Texas, and at Chico, California; also under winter protection at San Antonio, Texas. Almost no injury occurred to it at Chico even in 1913 except that the plants were badly bent down by the weight of the snow. At both Brownsville and Chico seedlings of the species have been grown to maturity under outdoor conditions and they are indistinguishable from the parent plants, which are vegetatively propagated from the type collection.

Opuntia Maideni sp. nov.

An erect to ascending, spreading, rather compactly branched, hemispherical shrub 1–1.5 m. in height; joints obovate, about 9 x 18 cm. at one year of age, at first raised at areoles and slightly so the second year, rather light, glaucous green; areoles broadly obovate, 4 mm. long, enlarging and becoming subcircular in age, tawny, becoming dirty black; leaves short, subulate, terete, cuspidate, pointed, 5 mm. long; spicules yellow, in a compact, 2 mm. tuft in upper portion of the areole, but surrounded above by a narrow zone of tawny wool, increasing to 3 mm. in length and occupying the entire areole in age; spines at first yellowish, turning white, very variable in all characteristics, sometimes the second year 1 or 2, sometimes none, 1 cm. long or less, or again they may be 4 in number and 3 cm. long, flattened and twisted, not increasing much in numbers on old wood, but often becoming 4 cm. in length; buds sharp-pointed, light green with appressed segments; flowers yellow, slightly greenish within, filaments greenish below, yellow distally, style bright deep red above, white below, stigma deep green, 7-parted, petals obovate to cuneiform, rounded, cuspidate above, about 28 x 40 mm.; fruits obovate to subglobose, deeply pitted, 2.5 x 3 cm., bearing about 15 areoles which contain one central tuft of yellow spicules 2 mm. long and 3 to 8 fugacious, hair-like spines, 1 cm. or less in length.

My knowledge of this perfectly characteristic species is derived from a specimen received from Professor J. H. Maiden, in whose honor it is named. He received it from some European collection. Its origin is unknown. I have received it from no other source. It was transmitted by Professor Maiden under No. 42 and is carried in our collections as M. 42. For years it was carried under protection at Chico, but for the past three years it has survived in the field without injury.

OPUNTIA BARTRAMI Raf.

Opuntia Bartrami Raf. Atlantic Jour. 1: 146. 1832.

An erect to ascending, rather strict and sparingly branched plant a meter or less high; joints elliptical to ovate, usually more or less pointed above and below; often 8 x 18 cm. or again small, 5 x 8 cm., often in current season's growth widest at middle and gradually narrowed each way, surface smooth, dark green, leaves conspicuous dull, reddish-green, 14–18 mm. long, somewhat curved outward; areoles subcircular to broadly obovate, 3 mm. long, brown; spicules yellow, in a compact tuft in central portion of

areole, 2–3 mm. long, increasing in age and filling entire areole; spines few, short, none or an occasional one, white to dirty gray, 3–5 mm. in length; flowers yellow, turning to orange-red when closed, but only slightly darker yellow at close of day; filaments orange, petals broadly obovate to spatulate about 26 x 45 mm., style white, stigma white, six-parted, small, rounded and minutely cuspidate above; fruit long, obovate, sometimes 24 x 55 mm., or often only 18 x 25 mm., dull, dark red, with the color extending only half way through the rind, interior being colorless.

This species is more or less common on the Florida Coast, in the region of New Smyrna. It is a rather striking thing, inasmuch as it is erect and strict in habit, and has few spines or may even be entirely spineless. The specimens from which the description is drawn have been carried by us under P. I. G. No. 13277, and were collected near New Smyrna, Florida, October 25, 1912, by Mr. R. A. Young. The specimens seem to me to be quite clearly referable to the Rafinesquean species, established in honor of the traveler Bartram.

The points upon which one must base judgment here are mainly four:—(1) habit and habitat of plant; (2) absence of spines; (3) color of fruit; (4) shape of joints. The same species was collected by myself at New Smyrna, Florida, several years before, and was grown to maturity at San Antonio, Texas, and Chico, California, but the number was lost. It is more than probable, however, that we still have that original collection of mine represented in No. 13777, P. I. G., which has been field-grown with us at Chico for a number of years, but with no record of its origin. It is identical with the one here described.

Opuntia obovata sp. nov.

A beautiful, glaucous, gray-green, erect species about 3–4 m. in height when fully developed, but blossoming profusely with us at 1 m. when grown from cuttings, rather widely branched but distinctly arborescent even in vegetatively propagated plants; joints long, obovate, broadly rounded above and gradually narrowed below, commonly 20 x 38 cm. or again frequently 15 x 35 cm., glaucous gray-green, turning yellowish green in age, raised at areoles when young and not losing tuberculation entirely until the third year; areoles brown, gray the second year and finally black, subcircular or triangular, abour 2.5 mm. in diameter, becoming enlarged on old trunks to frequently one cm. in diameter,

practically all armed; spicules yellow, invisible until third year and then in a small, compact, inconspicuous tuft in upper portions of areole, never conspicuous; spines white with translucent tips, flattened, twisted, not annular, becoming dirty gray, on last year's joints mostly 2 or 3 with 4 commonly on edges, the longest upper central one 3–3.5 cm. long, the others gradually smaller down to 8 mm. in length, on joints two years of age increasing about one to the areole and the longest are 3.5–4 cm. and the others in proportion and increasing even beyond this in both numbers and length, all rather stout; flowers yellow about 6 cm. in diameter, filaments greenish at base, style slightly tinged, stigma light greenish-yellow, 10-parted; fruit turning yellowish but soon approaching orange but not so deep as *naranjada* of the Mexicans, having a faint tinge of pink, long, obovate, with prominent dark brown areoles broadly obovate to subcircular and 3 mm. long, 15–16 mm. apart at the middle, more crowded and more elongated above, its spicules yellow, short, and central, surrounded by the 1 mm. long wool, subtended by 1 to 4 variable, mottled, delicate, fugacious, hairlike spines in the upper areoles.

This, which I collected at Hepasote, Mexico, is one of the finest fruited of the Mexican pears. The fruit is quite characteristic, palatable and belongs to the general "blanca-amarilla" groups. When first matured it is a typical "blanca" but soon it would pass more readily for "amarilla." It is a very spiny species, consequently I doubted whether it should have the common name "liso," but several peons, to whom we are always obliged to refer for common names, insisted that this is the one by which it is commonly designated. The pulp is readily separable from the seed and the nutritive materials, unlike "tuna cardona" (*O. streptic antha*) is held in solution. When the pulp is removed preparatory for eating it is considerably red-colored in the rind and both the interior and exterior of the pulp have a decidedly orange cast. It is a large sized tuna, commonly 5 x 9 cm., and slightly to deeply pitted. The species has not been seriously injured by cold at Chico except in January, 1913, when our stock was all reduced to cuttings. As frequently happens with these plants the articulation between the joints is weakened first and the trunks may be killed when the outer joints may be saved by planting after a period of recovery from the effect of cold.

The type is preserved under my collection No. 8071 and was secured at Hepasote, Mexico, in August, 1905. It has been in

cultivation with us since that date at both the Texas stations and Chico, California. At San Antonio, Texas, winter protection was necessary.

OPUNTIA MARITIMA Raf.

Opuntia maritima Raf. Fl. Med. 2: 247. 1830 (*nomen nudum*); Atlantic Jour. 1: 146. 1832.

A hemispherical shrub a meter or less in height with erect, ascending, or even reclining arms; joints obovate, about 10 x 17 cm., raised, tubercular at areoles, at first yellowish-green, but soon becoming glaucous gray-green, the tuberculation persisting for two or more years; leaves short, conical, 4–5 mm. long; areoles at first brown, subcircular or transversely elongated but finally elongated to 6 mm. on the sides of the joints and 3–4 mm. wide, on edges often becoming 4 x 7 mm.; spicules yellow in a crescentic tuft in center of areole, entirely surrounded by the brown wool, but later in an enlarged tuft occupying all of the upper part of the areole; spines 1 to 4, yellow, 1–2.5 cm. long, porrect, diverging but little; flower buds yellowish-green with closely appressed, short, wide floral segments; flowers yellow, turning to orange within at close of day, 6–7 cm. in diameter when opened, filaments greenish-tinged below, white above but becoming slightly tinged with red above at close of day, style white becoming tinged with red above at close of day, stigma white, 9-parted, subglobose to conical, truncate; fruit purplish-red throughout, pyriform, the stipe usually turning color tardily, about 46 x 80 mm., shallowly to deeply pitted. [PLATE 10.]

There appears to be no question but that the main coastal *Opuntia* of Florida is *O. maritima* of Rafinesque, although it does not appear to be so recognized in the literature. With reference to its affinity I will say that in my opinion it is more closely related to the South American group *O. inermis* DC. than any other. As the day advances the flower of this species turns to deeper yellow or almost orange within and to a deeper yellow in the distal portions of the petals as well. At the close of the day, or often early in the afternoon, the filaments and the apex of the style may show a slight tinge of reddish or orange-reddish, as is common in so many species. Color notes on *Opuntia* flowers are therefore of little value unless accompanied by an indication of the approximate time at which they were made.

It is a very prolific species, producing with us in California an

almost solid mass of fruit over the periphery of the plant. In Texas the growth is even more rampant, but the fruit production is much more restricted. It has been secured by us from various situations from the Carolinas to the east coast of Florida, and has been observed at one or two points on the west coast as well.

The specimen upon which this discussion is based has been carried under my inventory No. 8286, and was sent to me in 1906 by Mr. Harmon Benton from Georgia. He found it growing in a yard in Savannah.

Opuntia amarilla sp. nov.

A tall, open-branched tree 2.5–4 m. high with widely spreading branches, but in our cultivated plantation with vegetatively propagated plants not trimmed they are headed on the ground; joints glaucous blue-green, oval to obovate, mostly 17–20 x 35–38 cm. but very variable, turning slightly yellower and losing bloom, and becoming scaly black on old trunks; areoles brown, oval, 3 mm. long, abruptly raised the first season but flat later, enlarging in age to subcircular and 5–6 mm. in diameter; leaves conical, cuspidate, 3–4 mm. long, usually tinted at tip; spicules light yellow, inconspicuous or even invisible until late in the season, situated in a compact tuft in upper part of areole and not over 1 mm. long, more prominent at base of joints; spines white with translucent tips, porrect, diverging in all directions, on one-year-old joints usually 2 to 5, nearly all areoles armed, mostly 3 or 4, porrect, diverging in all directions, the central upper one reaching a maximum length of 3-4 cm., the lower 1 cm. long and the lateral ones midway between, increasing in number and length with age up to about 3 years, flattened, twisted, especially in age; buds rounded to bluntly pointed, dull dark olive with tinge of dull dark greenish-red at tip; flowers orange with darker center, having a tinge of red at base, filaments greenish below tinged with pink above, style red, stigma medium, dark green, 8-parted (one hour after anthesis), old flower turning deeper orange-red as day advances and distinct pinkish-red when closed; fruit large, obovate, 50–65 x 90–100 mm., at first turning yellowish but soon showing streaks and blotches of red in deeper tissues and finally becoming completely dull red with the stipe and the raised areoles at the apex usually remaining more or less yellow, even at complete maturity, rind yellowish and pulp light red; seeds medium sized, comparatively few in number and easily separable from the pulp, its areoles broadly obovate to subcircular, 2 mm. long, brown, 10–12 mm. apart with brown, prominent wool completely sur-

rounding the prominent tuft of yellow spicules which are 2–3 mm. long, all but lower areoles bearing 1, 2, 3 or 4 delicate, fugacious spines 5–12 mm. long.

This species secured in cultivation at Cardenas, Mexico, bears one of the finest fruits we have assembled in our entire collection. The species is characterized by its large, long, compact, glaucous joints and peculiarly colored fruits. At our Chico station it is not always hardy. We have, however, had plants of it fully 2 m. high with a spread of about equal dimensions. During the freeze of 1913 the plants went to the ground but we were able to save stock and at the present time (autumn, 1918) we have a number of individuals 2 meters in height and 2 meters in spread, loaded with fruit. One of the objections to the species in our plantations is its rather ungainly habit, which was overcome in the first planting made by a little pruning when the plants were young. No injury from cold has occurred excepting during the winter of 1913. In 1915 fruits of six of our best varieties were tested at Washington after shipment in mail packages from the Pacific coast. There was but one, which is probably an undescribed species, which scored ahead of this. The size, color, abundance and general attractiveness of this fruit always attract attention in our plantation.

UNITED STATES DEPARTMENT OF AGRICULTURE

Explanation of plates 9 and 10

PLATE 9

OPUNTIA DIVERSISPINA Griffiths. Showing both current and previous years growth toward the end of the growing season.

PLATE 10

OPUNTIA MARITIMA Raf. Showing young and mature joints, green fruits and buds.

The genus Desmatodon in North America

R. S. Williams

(WITH PLATE 11)

The work on this genus was mostly done some four or five years ago, but little has since occurred, so far as the author knows, to cause any important changes. Twelve species are here included in the genus as against thirteen in the Lesquereux & James Manual, but two of these thirteen species, *D. neomexicanus* and *D. nervosus* belong to *Tortula* while one other, *D. arenaceus*, is reduced to *D. obtusifolius*. This leaves ten of the Manual species, the two additions being *D. Sprengelii*, originally from Santo Domingo and discovered in Florida in 1916 by Dr. J. K. Small, and *D. stomatodontus* from Jalisco, Mexico.

Desmatodon Bushii Card. & Thér., from Missouri, belongs to *Tortula*, *fide* Brotherus; *D. Sartorii* (C. Müll.) Paris, from Mexico, is a *Leptodontium*; and *D. systylioides* Ren. & Card., from Newfoundland, a *Pottia*.

DESMATODON Brid. Musc. Recent. Suppl. 4: 86. 1819

Plaubelia Brid. Bryol. Univ. 1: 522. 1826.

Trichostomum § *Desmatodon* C. Müll. Syn. 1: 588. 1849.

Didymodon § *Desmatodon* Kindb. Eur. & N. Am. Bryin. 2: 273. 1897.

Dioicous or monoicous. Mostly alpine plants of medium or small size, usually growing in rather compact cushions on moist earth. Stems, mostly with central strand, simple or somewhat branching, closely leaved and more or less radiculose. Leaves erect-flexuous and appressed when dry; ovate and oblong to oblong-lanceolate or somewhat spatulate, concave, the margins flat, recurved or broadly incurved, entire or slightly serrulate in the upper part, sometimes colored or thickened, the apex mostly broadly acute, with costa vanishing below the apex, percurrent or excurrent into a short awn or elongate, nearly smooth hair-point. Costa in cross-section usually showing two or four guide-cells, one or two rows of large cells on the ventral side and on the dorsal side, a large stereid band, with outer cells more or less

differentiated. Cells of upper part of leaf mostly quadrate to hexagonal, scarcely or not elongate, obscure, densely papillose on both sides or distinct and more or less mamillose; those of lower part of leaf, pale, smooth and elongate-hexagonal to rectangular. Perichaetial leaves usually not greatly differentiated. Seta erect, often strongly twisted. Capsule oblong to cylindric, erect or nodding and curved, with stomata mostly few, in the basal part, the columella often projecting above the rim; the lid conic to more or less beaked. Annulus compound, often persistent. Peristome densely papillose, the sixteen teeth (sometimes scarcely developed in *D. obtusifolius*) from a basilar membrane usually extending well above the annulus, mostly divided to near the base into two or three slender, erect or oblique forks, or the forks sometimes quite irregular and more or less united above. Calyptra cucullate, descending well below the lid.

Type species: *Dicranum latifolium* Hedw.

Capsule erect and symmetric or nearly so; leaf margin of one thickness of cells.
- Cells of upper part of leaf more or less densely papillose with variously shaped papillae.
  - Leaf-margins somewhat recurved and leaves hair-pointed (except in *D. latifolius muticus* which is distinguished from *D. obtusifolius* by the leaves with margins partly flat and twice as long, 2.5–3 mm., and by the spores, 20 μ instead of 8–10 μ); the older leaves without a distinct golden-brown border.
    - Monoicous.
      - Upper leaves with blade usually 2–3 mm. long.
        - More or less spatulate or oblong, the upper marginal cells mostly obscure and rough with numerous papillae. 1. *D. latifolius.*
        - Gradually tapering from below the middle to an acute point. 2. *D. suberectus.*
      - Upper leaves with blade 1.5 mm., or less, long, the upper marginal cells distinct with few or no papillae. 3. *D. Guepini.*
    - Dioicous; blade of leaf about 2.5 mm. long. 4. *D. plinthobius.*
  - Leaf-margins mostly strongly revolute all round and leaves not hair pointed. 5. *D. obtusifolius.*
  - Leaf-margins flat, the older leaves with a distinct, golden-brown border. 6. *D. Porteri.*
- Cells of upper part of leaf never papillose, distinct, mostly mamillose on one or both sides.
  - Median leaf-cells 15–20 μ and spores about 25 μ in diameter. 7. *D. systilius.*

Median leaf-cells and spores 8–10 μ, or less, in diameter.
Leaf-cells highly mamillose on the upper surface, mostly flat on under side, the leaves slightly serrulate toward apex.
Leaves oblong-lanceolate, acute; costa slightly excurrent. 8. *D. Garberi.*
Leaves oblong-linear, the apex broadly rounded or broadly acute; costa vanishing 2–3 cells below the leaf-apex. 9. *D. Sprengelii.*
Leaf-cells mamillose on both sides; margins of the leaf crenulate half way down or more. 10. *D. stomatodontus.*
Capsule nodding, more or less curved; leaf-margins thickened.
Cells of lid scarcely elongate, in erect rows. 11. *D. cernuus.*
Cells of lid a little above the base elongate in oblique rows. 12. *D. Laureri.*

1. DESMATODON LATIFOLIUS (Hedw.) Brid. Musc. Recent. Suppl. 4: 86. 1819

Dicranum latifolium Hedw. Descr. 1: 89. 1789.
Barbula latifolia Kindb. Eur. & N. Am. Bryin. 2: 252. 1897.

Autoicous, the male flower on a short stalk a little below the perichaetium with numerous club-shaped paraphyses surrounded by one or more broadly pointed, scarcely longer leaves: fertile plants in rather soft, green or brownish green tufts, reddish tomentose within; stems with central strand, erect, often branching, from a few mm. to 2 cm. high; upper stem-leaves more or less ovate or obovate to somewhat spatulate, the blade usually 2.5–3 mm. long and 1 mm. wide, mostly broadly acute, with costa nearly percurrent or excurrent into a terete, not quite smooth hair-point (or in var. *muticus* the hair-point lacking), the lower leaves smaller with costa vanishing below the apex; leaf-margins papillose, otherwise entire and more or less revolute on one or both sides; costa in cross-section showing mostly two large guide-cells, three or four cells nearly as large on ventral side, and on dorsal side a more or less distinct stereid band with two to four large outer cells; cells of upper part of leaf mostly square to short-rectangular, obscure with numerous round to oblong and c shaped papillae; perichaetial leaves scarcely differentiated; seta erect, twisted when dry, 1–1.5 cm. long; capsule erect, oblong to cylindric, 1–2 mm. long; annulus of one to three rows of cells, more or less persistent; peristome golden brown, densely papillose, the basal membrane extending well above the annulus, with teeth mostly split to near the base into two or rarely three slender, erect forks, or the forks sometimes united above and slit below; lid obliquely beaked, one third to one half the length of the rest of

the capsule, the cells near the base not elongate, those further up broadly oblong, in erect rows; calyptra smooth, cucullate, descending well below the rim of capsule; spores papillose, rather irregular, the larger 20–24μ in diameter. [FIG. 1.]

TYPE LOCALITY: Sweden or Lapland.

DISTRIBUTION: Greenland; Gaspé coast of Canada to Unalaska and southward to California and New Mexico.

EXSICCATAE: Aust. Musci App. *123*.

ILLUSTRATION: Sull. Ic. Musc. Suppl. *23*.

The var. *glacialis* Schimp. is evidently not distinct from the var. *muticus* Brid.

2. DESMATODON SUBERECTUS (Hook.) Limpr. in Rab. Krypt.-Fl. 4^1: 651. 1889

Tortula suberecta Hook. in Drummond, Musci Am. *145*. 1828.

Desmatodon obliquus B.S.G. Bryol. Eur. (18–20): Desmatodon 10. 1843.

Paroicous, the antheridia usually four or five with few, nearly filiform and somewhat longer paraphyses, in a cluster just below the archegonia: plants in rather dull green tufts with branching stems, 0.5–1 cm. high; leaves rather broadly ovate-lanceolate, the upper larger, 2–3 mm. long and 1 mm. wide, gradually tapering from below the middle to an acute apex and terminating in a nearly smooth awn usually less than 0.25 mm. long, the leaf margins crenulate-papillose and mostly recurved: costa stout, excurrent into the point, in cross-section mostly showing two large guide-cells, two rows of somewhat smaller cells on ventral side and on dorsal side a large stereid band with scarcely differentiated outer cells; cells in upper part of leaf from square to hexagonal, 12–16 μ in diameter, usually obscure with numerous, minute, often C-shaped papillae on both sides, those of lower part smooth, pale, mostly rectangular; perichaetial leaves scarcely differentiated; seta up to 18 mm. long; capsule oblong-cylindric, mostly slightly curved and nodding, about 2 mm. long without lid, the stomata in two rows near the base; annulus of one or two rows of small, persistent cells; peristome teeth sixteen, usually divided to near the base into two or three slender, papillose forks, or sometimes the forks more or less united, mostly twisted about half way round, from a basilar membrane extending well above the annulus and composed of very elongate cells with thick, projecting walls; lid high-conic, the cells just above the base elongate in very oblique rows; calyptra extending about half way down the capsule; spores rough, up to about 22 μ in diameter. [FIG. 2.]

TYPE LOCALITY: Rocky Mountains of British America.

DISTRIBUTION: Greenland; Beechey Island, Arctic America; the Canadian Rockies; also in Europe.

EXSICCATAE: Drummond, Musci Am. *145*.

ILLUSTRATION: B.S.G. Bryol. Eur. *pl. 136*.

3. DESMATODON GUEPINI B.S.G. Bryol. Eur. (18–20): Desmatodon 8. 1843

Trichostomum Guepini C. Müll. Syn. 1: 590. 1849.
Barbula Guepini Schimp. Syn. ed. 2, 197. 1876.
Tortula Guepini Broth. in E. & P. Nat. Pfl. 1^3: 430. 1902.

Autoicous, the two or three very small male flowers scattered along the stem and composed of four or five pale, ecostate, ovate, acute leaves, smooth or nearly so, the outer longer ones about 0.5 mm. long, enclosing three or four antheridia about 0.25 mm. long, with few or no paraphyses: fertile plants rather loosely cespitose, bud-like, 1–3 mm. high; the larger upper leaves ovate to somewhat spatulate, with blade 1–1.5 mm. long, the apex somewhat rounded or acute, the margins entire and revolute from near the apex almost to base and the costa mostly smooth on the back, excurrent into a nearly smooth point one fifth to one half the length of the blade; costa in cross-section showing mostly two guide-cells, four or five cells of about the same size in one row on the ventral side and on the dorsal side a thick stereid band with outer cells differentiated; leaf-cells rather obscure and densely papillose in upper part of leaf, more or less four to six sided, not or scarcely elongate, 14–16 μ wide, those of basal part smooth, pale, larger, more or less rectangular: outer perichaetial leaves not differentiated, the inner small, acutely pointed, with flat margins; seta erect, about 8 mm. long; capsule erect, oblong-cylindric, 1–1.5 mm. long without lid, the stomata in one row near the base; annulus narrow, persistent, of one or two rows of cells; peristome pale, densely papillose, of sixteen slightly oblique, narrow teeth mostly divided nearly to the base into two filiform forks from a basilar membrane extending well above the annulus; lid high-conic, its height about twice the basal diameter, the cells a little above the base elongate in nearly erect rows; spores nearly smooth, the larger 16μ in diameter; calyptra cucullate, descending about half way down the capsule. [FIG. 3.]

TYPE LOCALITY: France.

DISTRIBUTION: California and France.

ILLUSTRATION: B.S.G. Bryol. Eur. *pl. 133*.

4. DESMATODON PLINTHOBIUS Sull. & Lesq. Musci Bor. Am. *94*. 1856

Desmatodon neomexicanus Sull. & Lesq. Musci Bor. Am. *95*. 1856.

Dioicous, the male plants very similar to, and mixed with, the fertile tufts, the flowers terminal or lateral by innovations from just below the apex; the inner perigonial leaves short; acute, with pale, smooth cells extending two thirds way up the leaf, the antheridia often numerous, about 0.33 mm. long, with abundant, filiform paraphyses: fertile plants in compact cushions, with somewhat branching stems, 3–4 mm. or rarely 1 cm. high; leaves incurved-imbricate when dry, erect-spreading when moist, from oblong-lanceolate to narrowly lingulate with apex acute or rounded, those on lower stem with blade less than 1 mm. long with short point, on upper stem the blade up to 2.5 mm. long with a flexuous, smooth hair-point often of nearly equal length, the margins entire and mostly revolute from near the apex to below the middle; costa papillose on the back in upper part of leaf, in cross-section showing about four guide-cells with one or sometimes two rows of cells nearly as large on ventral side and on dorsal side a large stereid band with outer cells scarcely differentiated; cells of upper part of leaf obscure, somewhat four-sided, not elongate, about 8 μ wide, covered on both sides with very small, irregular, often C-shaped papillae, those of lower part rectangular, pale, smooth, up to 16 μ wide by 40 μ long; perichaetial leaves scarcely differentiated; seta erect, 6–12 mm. long; capsule oblong to nearly cylindric, erect, up to 3 mm. long without lid; the lid rather obtusely high-conic, 0.5–0.7 mm. long, the two or three basal rows of cells not elongate, those about one third above the base two or three times longer than wide, in slightly oblique rows; peristome teeth pale, densely papillose, erect, mostly very irregular, sometimes scarcely projecting above the annulus, or longer and quite regularly divided into two forks from a low basilar membrane; annulus large, two or three rows of cells in height; calyptra cucullate, long-beaked, descending about half way down the capsule; spores smooth, about 8 μ in diameter. [FIG. 4.]

TYPE LOCALITY: Charleston, South Carolina.

DISTRIBUTION: Pennsylvania to Alabama and westward to Missouri and Texas.

EXSICCATAE: Sull. & Lesq. Musci Bor. Am. *94*, *95* (as *D. neomexicanus*) and ed. 2, *123*; Aust. Musci App. *493*.

ILLUSTRATION: Sull. Ic. Musc. *pl. 30*.

5. DESMATODON OBTUSIFOLIUS (Schwaegr.) Jur. Laubm. Oesterr. Ung. 135. 1882

Barbula obtusifolia Schwaegr. Suppl. 1: 129. 1811.
Desmatodon oblongifolius Hook. in Drummond, Musci Am. *114*. 1828 (*nomen nudum*).
Tortula obtusifolia Schleich.; Broth. in E. & P. Nat. Pfl. 1^3: 430. 1902.
Desmatodon arenaceus Sull. in Gray, Man. ed. 2, 628. 1856.
Desmatodon ohioense Schimp. Syn. 159. 1860.
Desmatodon subtorquescens C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 48. 1892 (apparently).
Didymodon arenaceus Kindb. Eur. & N. Am. Bryin. 277. 1897.

Apparently dioicous, the male plant much like the fertile but the terminal flower forming a more distinct rosette, the perigonial leaves scarcely differentiated, enclosing ten to twelve oblong antheridia 0.2 mm. long with nearly filiform, slightly longer paraphyses (the European plants are said to become autoicous by the older male stems finally bearing archegonial flowers, a condition not observed in North American specimens): plants in compact cushions, 3-4 mm. to 1 cm. high, with stems more or less branching and radiculose at the base; leaves of lower stem very small, gradually larger upward, the upper 1–1.5 mm. long and 0.25-0.5 mm. wide, oblong-lingulate, broadly acute and somewhat apiculate or rounded and blunt at apex, the margin more or less revolute nearly all round and entire or slightly crenulate in the upper part; costa stout, vanishing a little below the apex or percurrent, smooth on the back or papillose in the upper part, in cross-section showing two to four guide-cells with one or two layers of somewhat smaller cells on the ventral side and on the dorsal side mostly a distinct stereid band with outer cells slightly or not differentiated; cells in upper part of leaf mostly obscure, densely papillose with partly C-shaped papillae, more or less four-sided, about 8 μ in diameter, those of lower part pale, smooth, about 12 μ wide and from nearly square to two or three times longer than wide; perichaetial leaves about like those of stem, the inner sometimes smaller; seta erect, up to 1 cm. long, often strongly twisted below to the left and above to the right; capsule nearly straight and erect, 2 mm. long, with stomata in one row in the short, scarcely distinct neck; peristome variable, pale to reddish brown, finely papillose throughout, the basilar membrane extending usually a little above the rim of the capsule and either bearing slightly oblique teeth once or twice divided into slender forks of unequal

size or sometimes the teeth reduced to short irregular lobes, scarcely evident above the persistent annulus of about two rows of cells; lid high-conic or shortly beaked, the cells in slightly oblique rows and mostly elongate about half way up the lid; spores smooth, up to 10 μ in diameter; calyptra cucullate, descending to about the middle of capsule. [FIG. 5.]

TYPE LOCALITY: Switzerland.

DISTRIBUTION: New Brunswick to Vancouver Island and southward to Ohio, Missouri, Arizona, and California; also in Europe, Turkestan and Africa.

EXSICCATAE: Sull. & Lesq. Musci Bor. Am. *93*, *120*; Holz. Musci Acro. Bor. Am. *17*.

ILLUSTRATIONS: Schwaegr. Suppl. 1: *pl. 129*; B.S.G. Bryol. Eur. *pl. 133*. Sull. Ic. Musc. *pl. 29*.

6. DESMATODON PORTERI James in Aust. Musci App. *123*. 1870

Barbula subcarnifolia C. Müll. & Kindb.; Macoun, Cat. Can. Pl. 6: 52. 1892.

Dioicous, male plants rather smaller than the fertile and mixed in with them, the flowers terminal or lateral by innovations from just below the apex, with outer antheridial leaves about 1 mm. long, broadly ovate-lanceolate, acute, papillose in upper part and costate, the inner leaves much smaller, pale, smooth, enclosing quite numerous antheridia about 0.2 mm. long with nearly filiform paraphyses: fertile plants in compact tufts with stems usually 2–3 mm. high; leaves spreading, flexuous or somewhat incurved when dry, the upper about 2 mm. long, mostly broadly ovate-lanceolate, the apex acute, the margins flat and in the older leaves rather distinctly yellowish-bordered from a little below the apex to near the base with two or three rows of somewhat larger more elongate cells, less densely papillose than those within or often smooth; in the younger leaves this border is scarcely evident or appearing only as a paler margin; costa percurrent, papillose on the back, in cross-section showing about four guide-cells with a row of three or four cells of about equal size on ventral side and on dorsal side a large stereid band with outer cells differentiated; cells of upper part of leaf mostly very obscure with minute, often C-shaped papillae, the median cells not elongate, somewhat four-sided, about 8 μ in diameter, those in the border about one half way down mostly elongate; the cells of lower one third of leaf pale, smooth, shortly rectangular or elongate-hexagonal; perichaetial leaves slightly differenti-

ated; seta erect, mostly 7–10 mm., rarely 13 mm. long; capsule erect, nearly straight and cylindric, about 2 mm. long without lid, with a conical more or less short-beaked lid 0.50–0.75 mm. long, the cells from a little above the base mostly oblong in slightly oblique rows; annulus large, persistent, of two or three rows of cells; peristome papillose, reddish or golden brown, the erect or nearly erect teeth from a basal membrane projecting a little above the annulus and irregularly divided into two or three forks, or the forks sometimes more or less united; spores smooth, about 8 μ in diameter; calyptra cucullate, long-beaked, extending one third way down the capsule. [FIG. 6.]

TYPE LOCALITY: Easton, Pennsylvania.

DISTRIBUTION: Gaspé coast, Quebec, and Point Pelee Island, Lake Erie, Ontario, to Pennsylvania, Ohio and Illinois.

EXSICCATAE: Aust. Musci App. *123*.

ILLUSTRATION: Sull. Ic. Musc. Suppl. *pl. 23*.

7. DESMATODON SYSTYLIUS B.S.G. Bryol. Eur. (18–20): Desmatodon, Suppl. 1. 1. 1843

Paroicous, the antheridia about 0.25 mm. long, in one or two pairs, without paraphyses, in the axils of the outer perichaetial leaves: plants cespitose, somewhat branching, usually 2–3 mm. high, often more or less bud-like; the upper stem leaves with blade about 1.5 mm. long and 1 mm. wide, broadly ovate, acute, the margins mostly flat and entire or slightly crenulate at apex and the costa excurrent into a nearly smooth, flexuous, hair-point of variable length; the costa in cross-section showing two guide-cells with two often larger cells on the ventral side and on the dorsal side a large stereid band with differentiated outer cells; cells of upper part of leaf from nearly square to rhomboidal or hexagonal, somewhat mamillose, the median 15–20 μ in diameter, in lower part mostly rather larger and elongate-hexagonal or short-rectangular; perichaetial leaves scarcely differentiated; seta erect, about 8 mm. long; capsule erect, oblong-cylindric, up to 2 mm. long without lid, the columella exserted, persistent, the stomata in about two rows near base; annulus persistent, of one or two rows of cells; peristome teeth reddish brown, papillose, mostly divided to near the base into two forks, erect from a rather low basal membrane; lid remaining more or less attached to the columella after separating from the annulus, obliquely short-beaked, the cells, except the three of four basal rows, elongate, in slightly oblique rows; calyptra cucullate, descending well down the capsule; spores rough, up to 25 μ in diameter. [FIG. 7.]

TYPE LOCALITY: Norway.

DISTRIBUTION: Greenland and Newfoundland to the Canadian Rocky Mountains and at the foot of Mount Dana, California; also in Europe.

ILLUSTRATION: B.S.G. Bryol. Eur. *pl. 131.*

8. DESMATODON GARBERI Lesq. & James, Man. 112. 1884

Hyophila fragilis Card. Rev. Bryol. 36: 75. 1909.

Dioicous, the male plants very slender, with a rosette-like apical flower, the outer perigonial leaves scarcely differentiated, the inner shorter, ovate-acute, entire, costate, enclosing ten to fifteen antheridia about 0.3 mm. long, with filiform, somewhat longer paraphyses: fertile plants in compact cushions with slender, erect, mostly unbranched stems 5–6 mm. high and about 0.2 mm. in diameter with distinct central strand and few or no radicles above the base; stem leaves rather distant, incurved or somewhat crispate and subtubulose when dry, the upper 1–1.5 mm. long, oblong-lanceolate, acute, with margins incurved and entire or occasionally with a few small teeth near the apex, flat and entire below; costa stout, sometimes rough on the back in the upper part, percurrent, in cross-section showing two to four guide-cells with one or two rows of smaller cells on the ventral side and on the dorsal side a large stereid band with outer cells scarcely differentiated; cells of leaf distinct, more or less golden brown from apex to base of leaf, those of upper part highly mamillose on the ventral side, mostly nearly flat on the dorsal side, the median cells roundish, about 8 μ in diameter, the basal smooth and rather short-rectangular; perichaetial leaves scarcely differentiated or sometimes one or two very small inner leaves; seta erect, 5 mm. long; capsule somewhat fusiform, its greatest diameter a little below the middle, 1–1.3 mm. long without lid, the stomata in one row near the base; annulus of one or two rows of cells; teeth of peristome reddish brown, papillose, irregular, divided often nearly to base into two slender forks, from a papillose basilar membrane scarcely extending above the rim of capsule; lid nearly erect, conical, short-beaked, about one third the length of the capsule, the cells elongate in nearly erect rows; spores smooth, 6–8 μ in diameter, calyptra cucullate, extending well down the capsule, sometimes split upward to near the smooth apex. [FIG. 8.]

TYPE LOCALITY: Key West, Florida.

DISTRIBUTION: New Providence, Bahama Islands; Key West, Florida; and Yucatan, Mexico.

The specimens of *Hyophila fragilis* are not fruiting but they do not seem to differ from *D. Garberi* except perhaps in being a little more slender.

9. **Desmatodon Sprengelii** (Schwaegr.) comb. nov.

Barbula Sprengelii Schwaegr. Suppl. 2^1: 64. 1823.
Plaubelia tortuosa Brid. Bryol. Univ. 1: 522. 1826.
Weisia Berteriana Spreng. Syst. Veg. 4: 156. 1827.

Dioicous, the male flower terminal, the short, inner antheridial leaves closely surrounding about six large antheridia, one third mm. long, with few, filiform paraphyses: fertile plants low, in dusky green cushions with simple, slender stems mostly 4–5 mm. long; leaves on the stem below rather distant, gradually and slightly larger and more crowded toward the apex, incurved when dry, widely spreading when moist, the upper about 1 mm. long, oblong linear, with broad, somewhat rounded or broadly acute, slightly apiculate and serrulate apex, the margins from a little below the apex to the middle of leaf or farther, incurved and entire; costa stout, often slightly rough on the back near the apex and the ventral surface more or less mamillose, vanishing two or three cells below the apex of the leaf, in cross-section showing two or three guide-cells with an equal number of somewhat smaller cells on the ventral side and on the dorsal side a stereid band with outer cells differentiated; cells of upper part of leaf distinct, roundish-hexagonal, 6–7 μ in diameter, mamillose on the upper side, flat or nearly so on the under side, in about the lower fourth of leaf becoming square to short rectangular with colored, slightly thickened walls as in cells of upper leaf; perichaetial leaves mostly a little longer than those of the stem with a somewhat broader, loosely clasping base rather gradually narrowed to a not quite entire, more acute point; seta erect, about 4 mm. long; capsule erect, somewhat fusiform, about 1.5 mm. long without lid, the exothecal cells rather irregular, two to four times longer than broad, with thin walls, the stomata few, near the base; peristome reddish brown, the basal membrane extending about the height of the annulus above the rim, with 16 erect, quite irregular, finely papillose teeth of variable length either undivided or more or less divided along the median line; lid somewhat obliquely subulate, about two thirds the length of the rest of the capsule; spores about 8 μ in diameter, pale and smooth; calyptra cucullate, extending about half way down the capsule. [FIG. 9.]

TYPE LOCALITY: Hispaniola (Santo Domingo).

DISTRIBUTION: known only from Santo Domingo and Florida (Cape Sable, 1916, *J. K. Small*).

10. **Desmatodon stomatodontus** (Card.) comb. nov.

Hyophila stomatodonta Card. Rev. Bryol. **36**: 76. 1909.

Dioicous: plants with slender stems 4–8 mm. long; lower leaves minute, the larger crowded into a rosulate tuft at the apex of the stem, somewhat spatulate-oblong, flexuous with strongly inrolled margins when dry, more or less widely spreading when moist, about 1.5 mm. long, mostly obtuse and scarcely apiculate, the margins finely crenulate to below the middle; costa percurrent, 40 μ wide a little above the base, in cross-section showing two large guide-cells, three to four rather large cells above them and below a large stereid band with the outer cells differentiated; cells in upper part of leaf distinct, roundish to hexagonal, mamillose on both sides, 6–8 μ in diameter, in the lower leaf, square to short-rectangular and scarcely paler than above; one or two inner perichaetial leaves sometimes lanceolate, acute, with the costa scarcely percurrent; seta about 5 mm. long; capsule erect, cylindric, about 1.5 mm. long without lid, the exothecal cells mostly irregularly elongate, with thin walls, the median cells about 20 μ wide by 40–50 μ long; lid about one-half the length of the capsule, nearly erect, with cells a little above its base elongate in nearly erect rows; annulus large; peristome reddish brown, papillose, fragile, irregularly divided from some distance above the rim into slender forks extending about 150 μ above the rim; spores smooth, pale, 7–8 μ in diameter. [FIG. 10.]

TYPE LOCALITY: State of Jalisco, Mexico.

DISTRIBUTION: known only from type locality.

11. DESMATODON CERNUUS (Hueb.) B.S.G. Bryol. Eur. (18–20): Desmatodon 8. 1843

Dermatodon cernuus Hueb. Musc. Germ. 117. 1833.

Cynodontium latifolium Schwaegr. Suppl. 1[1]: 110. 1817 (not *Dicranum latifolium* Hedw. Desc. **1**: 89. 1787).

Desmatodon camptothecius Kindb.; Macoun, Cat. Can. Pl. 6: 48. 1892.

Dermatodon camptothecius Kindb. Eur. & N. Am. Bryin. **2**: 283. 1897.

Autoicous, the male flower just below the perichaetium, composed of several club-shaped, often long-stalked antheridia, with rather numerous, slightly club-shaped paraphyses, enclosed by two ovate-lanceolate, costate leaves about 1 mm. long, either entire or with one or two rather large teeth at the acute apex: plants in compact cushions with mostly simple stems from 3–4

mm. up to 2 cm. high; stem leaves more or less erect or flexuous and twisted when dry, from oblong-linear to oblong-spatulate, up to 3.5 mm. long by 1 mm. wide, acute, the margins toward apex flat and mostly not quite entire, of a single layer of cells, farther down more or less revolute on one or both sides and usually of a double layer of two to four rows of slightly colored cells; costa smooth on the back, mostly excurrent into a short awn, in cross-section showing two guide-cells, a single row of about three cells nearly as large on the ventral side and on the dorsal side a stereid band with the outer cells differentiated; cells of upper part somewhat rhomboidal to hexagonal, up to 20 μ wide by 25 μ long, rarely smooth or nearly so but mostly papillose on both sides; cells of lower part smooth, lax, pale, up to 30 μ wide by 140 μ long; perichaetial leaves scarcely differentiated; seta erect, 1.5–2 cm. long, yellow or finally reddish; capsule nodding to horizontal, somewhat curved-ovate, the mouth rather small and oblique, the few stomata in one row at the base; peristome reddish brown, densely papillose, the teeth mostly divided irregularly into two forks, one or both of which are more or less perforate or split in the lower part, the basilar membrane extending well above the rim; annulus persistent, of one to three rows of rather small cells; lid obliquely short-pointed, its height slightly exceeding its basal diameter, the cells in erect rows and scarcely elongate except in the point; calyptra cucullate, rather small, the apex smooth and dark colored; spores papillose, 30–50 μ in diameter. [FIG. 11.]

TYPE LOCALITY: Tyrol, Austria.

DISTRIBUTION: Gaspé coast, Quebec, to the Yukon River, and southward to Colorado.

EXSICCATAE: Macoun, Can. Musci *71*, *604*.

ILLUSTRATIONS: Schwaegr. Suppl. 1^1: *pl. 28*; B.S.G. Bryol. Eur. *pl. 134*.

12. DESMATODON LAURERI (Schultz) B.S.G. Bryol. Eur. (18–20): Desmatodon 9. 1843

Trichostomum Laureri Schultz, Flora **10**: 163. 1827.

Tortula bryoides Hook. in Drummond, Musci Am. *135*. 1828.

Autoicous, the male flower sessile just below the perichaetium, of eight or ten more or less stalked antheridia about 0.5 mm. long, with abundant, often longer, club-shaped paraphyses, enclosed by two or three ovate, entire, somewhat acute leaves, with the costa vanishing just below the apex: plants in compact tufts from a few millimeters to 2 cm. high, with somewhat branching stems more or less tomentose below; the lower stem leaves ovate, the upper longer, more or less erect-flexuous and twisted when dry, nearly

linear, the base often a little broader, 4 mm. long and 1 mm. wide, rarely 5.5 mm. long and 1.5 mm. wide, the point rounded or broadly acute and mostly apiculate by the shortly excurrent costa; leaf-margin, except near the flat and not quite entire apex, with a distinct, thickened and recurved border extending to near the base; costa papillose on the back to below the middle, in cross-section showing two or three guide-cells, usually a single layer of large cells on ventral side, but sometimes two layers, and on dorsal side a large stereid band with outer cells somewhat differentiated; cells of upper part finely papillose on both sides, rhomboidal to hexagonal, the median about 16 μ wide by 18–25 μ long, the basal cells, often 20 μ wide by 50–80 μ long, smooth and more or less tinged with golden brown: perichaetial leaves scarcely differentiated; seta somewhat flexuous, 8–15 mm. long; capsule nodding to horizontal, sometimes pendant, oblong, more or less curved, up to 2 mm. long without lid, the stomata in one row at the base; peristome reddish brown, the distantly articulate teeth often twisted almost once around and divided nearly to the base into two or three slender, terete, sometimes split or perforate forks or the forks sometimes united above; annulus persistent, of two or three rows of small cells; lid conic, short-pointed, the three or four basal rows of cells not elongate, those above elongate-rectangular, in very oblique rows; calyptra cucullate, extending about one half way down the capsule; spores papillose, 30–40 μ in diameter. [FIG. 12.]

TYPE LOCALITY: Tyrol, Austria.

DISTRIBUTION: Rocky Mountains of British America and Vancouver Island to Colorado; also in Greenland, Europe and Asia.

EXSICCATAE: Drummond, Musci Am. *135*.

ILLUSTRATION: B.S.G. Bryol. Eur. *pl. 135*.

Explanation of plate 11

Cross-sections of *Desmatodon* made about half way down the leaf.

FIG. 1. *Desmatodon latifolius* (Hedw.) Brid., from California, × 270.

FIG. 2. *Desmatodon suberectus* (Hook.) Limpr., from Canada, × 270.

FIG. 3. *Desmatodon Guepini* B. S. G., from California, × 270.

FIG. 4. *Desmatodon plinthobius* Sull. & Lesq., from South Carolina, × 270.

FIG. 5. *Desmatodon obtusifolius* (Schwaegr.) Jur., from Montana, × 270.

FIG. 6. *Desmatodon Porteri* James., from Pennsylvania, × 200.

FIG. 7. *Desmatodon systylius* B. S. G., from Labrador, × 270.

FIG. 8. *Desmatodon Garberi* Lesq. & James, from Florida, × 270.

FIG. 9. *Desmatodon Sprengelii* (Schwaegr.) R. S. Williams, from Santo Domingo, × 270.

FIG. 10. *Desmatodon stomatodontus* (Card.) R. S. Williams, from Mexico, × 350.

FIG. 11. *Desmatodon cernuus* (Hueb.) B. S. G., from Canada, × 270.

FIG. 12. *Desmatodon Laureri* (Schultz) B. S. G., from Colorado, × 270.

Notes on trees and shrubs in the vicinity of Washington

W. W. Ashe

There are a number of trees and shrubs which are apparently not recorded* as occurring in the vicinity of Washington, D. C., but which the writer has collected within distances which should allow inclusion in its flora. Several interesting forms of *Amelanchier* are included in this number and also several species belonging to various other genera.

Species and varieties of Amelanchier

The catalogue of the Washington Botanical Club credits four species of *Amelanchier: A. canadensis* (L.) Medic. (*A. Botryapium* Aut.), *A. laevis* Wiegand (*A. canadensis* Aut.), *A. oblongifolia* (T. & G.) Roem., and *A. stolonifera* Wiegand (?*A. nantucketensis* Bicknell). *A. laevis* is not common near Washington, but another associate of *A. canadensis*, which McAtee† has seemingly correctly referred to *A. intermedia* Spach, is frequent; this form so intergrades with *A. canadensis* that it should probably be regarded as a variety of that species. In addition to these *A. sanguinea* (Pursh) DC. occurs along the Potomac at Great Falls, Virginia, and growing with it are two other unrecorded forms. The first of these is here proposed as new; the second seems to be a hybrid or of hybrid origin and approaches *A. oblongifolia* var. *micropetala* Robinson,‡ the hybrid origin of which has already been suggested by Wiegand.§ Robinson's variety is here raised to specific rank and the form in question referred to it as a variety.

Amelanchier canadensis intermedia (Spach.) comb. nov.

Amelanchier intermedia Spach, Hist. Veg. Phan. **2**: 85. 1834.

Differs from the type in its smaller and usually less pubescent leaves, which are slightly bronze when unfolding; and in having

* The species in question are not mentioned in the Botanical Club's letter press catalogue; in Ward's Guide to the flora of Washington and vicinity; in any of the five supplements to that work; or, seemingly, in any subsequent publication.

† Biol. Soc. Washington, Bull. 1: 79. 1918.

‡ Rhodora 10: 33. 1908.

§ Rhodora 14: 133. 1912.

smaller flowers with narrow, often acute petals and a slightly larger hypanthium with very narrow sepals.

Frequent in bogs near Beltsville, Maryland.

AMELANCHIER SANGUINEA (Pursh) DC.

On shaded rocks along the Potomac River, at Great Falls, Virginia, ten specimens noted.*

Amelanchier sera sp. nov.

A shrub 1.2–4 m. high with habit (single-stemmed and bushy topped) much like that of small specimens of *A. canadensis*. Leaves 3–6 cm. long, 2.5–4 cm. wide, ovate or elliptic, rounded or subcordate at the base, obtuse or rounded and abruptly apiculate at the apex (the upper leaves on the twigs differing in being obovate and cuneate at the entire base), rather distantly serrate with short apiculate teeth, prominent veins in six to eight pairs, surface thickly coated with a grayish tomentum and more or less bronze colored upon unfolding, becoming nearly or quite glabrous at maturity, thick and firm, dark blue-green and lucid above, pale and glaucescent beneath, turning dark crimson in autumn; petioles one fourth to one third as long as the blades, often reddish at the base. Flowers appearing in late April and early May, in six- to eleven-flowered nodding racemes, 4–6 cm. long; petals oblong-spatulate, acute, 8–11 cm. long, 2.5–3 mm. wide; hypanthium small, 6–7 mm. across, from tip to tip of sepals, shallow, glabrous within, tube becoming glabrous before the opening of the flowers; sepals sometimes remaining slightly pubescent within until fruit is half grown, reflexed after anthesis and remaining so on mature fruits; summit of ovary glabrous. Fruit in four- to eight-fruited racemes, globose, 4–6 mm. thick, dark reddish purple when ripe (latter half of June), the lower fruiting pedicels 2–2.5 cm. long.

On rocky banks along the Potomac River, Fairfax County, Virginia, and Montgomery County, Maryland.

This new species blooms just after *A. canadensis*, when *A. stolonifera* and *A. oblongifolia* are entirely through blooming and *A. sanguinea* is still in bloom. It grows in association with all four of these species and also with the new variety to be described below. From *A. canadensis* (and also *A. laevis*) it is separated by its much smaller flowers, later blooming, more shallow hypan-

* Not included in McAtee's list of characteristic plants of Great Falls, *op. cit.* 107.

thium, and red (not yellow) autumnal foliage; from *A. oblongifolia*, by its darker green, more lucid, and relatively broader leaves, later blooming, and reflexed (not ascending) sepals; from *A. stolonifera*, by its habit and size, later blooming, smaller calyx, glabrous hypanthium, and by the different color and texture of its leaves. The inflorescence of *A. sera*, on account of the numerous bright scarlet bracts, has a decidedly reddish aspect (resembling that of *A. saxatilis* Blanch.), until the bracts fall as the petals being to expand. For several seasons this plant was regarded as *A. laevis* forma *nitida* Wiegand,* but Dr. Wiegand, after examining a specimen, states that it is not his plant. Specimens are being deposited in several American herbaria.

Amelanchier micropetala (Robinson) sp. nov.

Amelanchier oblongifolia var. *micropetala* Robinson, Rhodora **10**: 33. 1908.

According to Wiegand the probable parents of this supposed hybrid are *A. oblongifolia* and *A. stolonifera*. The general distribution of the plant, however, the fact that it has been reported from points where the putative parents are not now known to grow,† and its local abundance in certain localities seem to justify disregarding its probable hybrid origin. *A. micropetala* is distinguished from *A. oblongifera* by its shorter, broader, firmer and somewhat darker leaves, and from both *A. oblongifolia* and *A. stolonifera* by its petals, which are scarcely half as long and yellowish or cream-colored instead of being white. Weatherby‡ considers the peculiar features of the petals may be due to the teratological condition known as staminody. The typical form of *A. micropetala* is known from eastern Massachusetts and Connecticut.

Amelanchier micropetala potomacensis var. nov.

A slender, stoloniferous shrub with the general size (3–10 dm. high), habit (forming small clumps) and leaf-shape of *A. stolon-*

* Rhodora **14**: 155. 1912.

† Dr. Macbride writes that the supposed parents do not grow within many miles of plants of *A. micropetala* collected by Mr. Weatherby.

‡ Rhodora **18**: 49. 1916.

ifera. Leaves ovate, elliptic or orbicular, 2.2–4.5 cm. long by 2–3.1 cm. wide, obtuse or rounded and abruptly acute at the apex, rounded or subcordate at the base, finely and sharply serrate above the middle with acute, ascending teeth, densely white-tomentose beneath when young but soon becoming glabrous on both sides, deep green but not lucid above, slightly pale beneath, coloring shades of red in autumn; ascending prominent veins in six to nine pairs; petioles from one third to one half the length of the blades. Racemes erect, straight, short, dense, seven- to ten-flowered, grayish villose on unfolding, the bracts pale tan, the erect lower pedicels 1.2 –1.8 cm. long in flower, 1.5–2.2 cm. long in fruit; hypanthium large, tube cup-shaped, villose without, usually tomentose within; sepals short from a broad base, ascending or erect after petals fall; petals five, 3–5 mm. long, 1–3 mm. broad, obovate on spatulate, yellowish white or dull yellow; blooming period extending on some plants from late April to late May. Fruit subglobose or depressed-globose, the summit of the ovary usually lanate, 6–10 mm. thick when fully mature (the last week in June except on some of the upper pedicels), sweet and juicy, purple-black without bloom, capped by the erect calyx lobes.

On rocky banks along the Potomac River, Fairfax County, Virginia. Specimens are being deposited in several herbaria.

The variety here proposed shows the remarkable small yellowish petals, which are characteristic of the typical *A. micropetala.* Its blooming period begins with that of *A. stolonifera* and *A. oblongifolia* but continues two weeks longer. It is further characterized by its very large hypanthium. Specimens were submitted to the Gray Herbarium for comparison with the var. *micropetala* Robinson, and Dr. J. F. Macbride, who made the comparison, reports that its leaves closely match some of the material from Connecticut, which "exhibits the very broad leaves of *stolonifera*." It is therefore probable that this material should be also referred to the var. *potomacencis.* In its Potomac station, the new variety blooms at about the same time as *A. sera,* with which it is associated. Its petals exhibit considerable variation in size, but no specimens were seen in which the number exceeded five or in which there was actual loss of the petal form, agreeing in these respects with the material of *A. micropetala* described by Weatherby. If the plant was originally a teratological form it would now seem from its local abundance to have become self-perpetuating.

MISCELLANEOUS SPECIES AND VARIETIES

In addition to the forms of *Amelanchier* discussed above the following trees and shrubs, which apparently have not previously been credited to the Washington flora, have been found growing either in the District of Columbia or in nearby parts of Virginia and Maryland.

Carya glabra hirsuta (Ashe) comb. nov.

Hicoria glabra hirsuta Ashe, Notes on hickories. 1896.
Carya ovalis hirsuta Sargent, Bot. Gaz. **66**: 247. 1918.

This tree is not uncommon on rocky wooded slopes along the Potomac River at Great Falls, Virginia, and should be included among the trees which are characteristic of its flora. It has not been reported previously from north of North Carolina.

QUERCUS PAGODA Raf. Alsog. Am. 23. 1838

Edges of swamps near North Chesapeake Beach, Maryland. Not before credited to the Washington flora, although known from as far north as the island of Nantucket, Massachusetts.

QUERCUS SHUMARDII Buckl.

Growing with the preceding but not previously credited to the Washington flora. Attention has recently been called to the fact that *Q. Schneckii* Britton is a synonym of this species.*

CRATAEGUS APPOSITA Sargent

Great Falls, Virginia. This and the following have apparently not before been reported from south of Delaware and Pennsylvania.

CRATAEGUS SMITHII Sargent

Growing with the preceding.

TILIA MICHAUXII Nutt.

Along the Potomac River from above Great Falls to below Marshall Hall, Virginia, but not before credited to the Washington flora.

* Bull. Charleston Mus. 14: 9. 1918.

TILIA NEGLECTA Spach

Growing with the preceding but in greater abundance, the largest specimens seen being eighteen inches in diameter and sixty feet high. Sargent* has recently called attention to this very distinct species, which for several years has been a puzzle, being regarded as a probable form of *T. Michauxii*.

FRAXINUS CAROLINIANA Mill.

Along the Potomac River, Virginia, opposite Washington, and apparently the northern limit of the species. The species is the most characteristic tree in several hundred acres of river swamp, but has apparently never been included in the Washington flora.

FOREST SERVICE,
U. S. DEPARTMENT OF AGRICULTURE.

* Trees at Mount Vernon 5 1917.

INDEX TO AMERICAN BOTANICAL LITERATURE

1908–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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Taxonomic studies in Vernonia and related genera

HENRY ALLAN GLEASON

In preparing the manuscript for the tribe Vernonieae, to be published in the North American Flora, several new species and varieties were recognized and a few nomenclatorial changes became necessary. One of the latter involves the erection of a new genus. Since the form ot the North American Flora demands relatively concise descriptions and permits no critical discussion, the present paper is issued in advance.

A variety, in the opinion of the writer, represents a group which is not worthy of specific rank, yet demands recognition in the intensive study of a species. In general, varieties are not admitted into the North American Flora. Specific descriptions are drawn broadly enough to include all the varieties, while the varietal names are cited among the synonyms. The same treatment will be used for the varieties published here.

Although this paper and the manuscript for the North American Flora have been prepared at the New York Botanical Garden and are based primarily on the collections there, the writer has been greatly assisted by material from many American herbaria and takes this opportunity of expressing his thanks: to Mr. C. C. Deam and Mr. J. Lunell for material from their private herbaria; to those in authority at the University of California, the Field Columbian Museum, the University of Illinois, the Iowa Agricultural College, the University of Kentucky, the University of

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Minnesota, the Ohio State University, and the University of Wisconsin for the loan of material; to the directors or curators of the Brooklyn Botanic Garden, the Gray Herbarium, the National Herbarium, the New England Botanical Club, and the Philadelphia Academy of Sciences for the facilities of their herbaria and libraries; to Dr. B. L. Robinson, Dr. J. M. Greenman, Mr. W. R. Maxon, and Mr. E. E. Watson for information, assistance, and criticism; and especially to the University of Michigan, where part of the work was done.

VERNONIA BORINQUENSIS Urban

In describing the species, Urban took as the type a form with hirsute achenes, resinous-dotted leaves, and short straight appressed hairs on the lower leaf surface. This is the commonest form in American herbaria. Urban's variety *Stahlii* covers a much rarer form with glabrous achenes and without resinous dots on the leaves. Two other forms also occur, which are deserving of varietal names.

Vernonia borinquensis resinosa var. nov.

Achenes glabrous; leaves conspicuously dotted with glands and resin on the lower surface: otherwise like the typical form of the species.

TYPE: *ex herb. E. W. D. Holway*, collected at Cayey, Porto Rico, January, 1911, and deposited in the herbarium of the New York Botanical Garden.

Vernonia borinquensis hirsuta var. nov.

Achenes hirsute; leaves densely sericeous-hirsute beneath with bent or curved hairs 2–4 mm. long, nearly or completely concealing the resinous dots; otherwise like the typical form of the species.

TYPE: *Britton, Stevens, & Hess 2471*, collected in a wooded valley, Rio de Maricao, Porto Rico, at an altitude of 500–600 meters, April 2, 1913, and deposited in the herbarium of the New York Botanical Garden. Field notes indicate that it is a vine, two meters long.

The species and its three varieties may be distinguished as follows:

Achenes hirsute; leaves with resinous dots or glandular pits on the lower surface.
- Pubescence of short, straight, appressed hairs seldom exceeding 0.5 mm. in length. — *V. borinquensis.*
- Pubescence on the lower leaf-surface of bent or curved hairs 2–4 mm. long. — *V. borinquensis hirsuta.*

Achenes glabrous.
- Glands on the lower leaf-surface present. — *V. borinquensis resinosa.*
- Glands on the lower leaf-surface none. — *V. borinquensis Stahlii*

VERNONIA SERICEA L. C. Rich.

Vernonia phyllostachya (Cass.) Gleason.

We are indebted to Ekman for the application of the correct name to this well-known species. Specimens in American herbaria show a great variation in the size, proportion, and density of pubescence of the leaves, without offering legitimate opportunity for the separation of varieties.

VERNONIA GNAPHALIIFOLIA Rich.

Until the last decade this species was poorly represented in American herbaria. The collections of the New York Botanical Garden now include an ample series of specimens, sufficient to give some idea of the range of variation within the species. On casual inspection, the specimens fall into two groups, characterized by wide and narrow leaves. The latter come from the provinces of Santa Clara, Camaguey, and Oriente, that is, from eastern Cuba; while the former are from Santa Clara, Havana, and Matanzas. The wide-leaved forms have leaves from 9 × 19 mm. to 21 × 51 mm., and the ratio of length to width varies from 2.1 to 3.4. The leaves of the narrow-leaved specimens range in size from 4 × 23 mm. to 14 × 61 mm., and their ratio from 3.2 to 5.7. They make accordingly a continuous series. In all cases the leaves are somewhat revolute and densely sericeous beneath. All specimens agree in the characters of inflorescence and flower-structure except one, *Shafer 2958*, from Holguin, Oriente, which lacks the resinous dots on the principal involucral scales.

Another specimen differs so much from the specific type that it may be described as a new variety.

Vernonia gnaphaliifolia platyphylla var. nov.

Leaf-blades broadly elliptic-ovate, less than twice as long as wide, flat, not revolute at the margin, closely and finely gray-tomentose beneath; otherwise resembling the typical form of the species.

TYPE: *Britton, Cowell, and Shafer 12,933*, collected at Ensenada de Mora, Oriente, March 26–29, 1912, and deposited in the herbarium of the New York Botanical Garden. It is described as a shrub, one meter high, and is the only broad-leaved representative of the species so far known from eastern Cuba. It is also the only specimen examined within the species without the revolute leaf-margin and with distinctly tomentose pubescence.

VERNONIA ICOSANTHA DC.

Ekman has pointed out the peculiar nomenclatorial confusion attached to this well-known species of the Lesser Antilles, and has chosen to apply to it the name *Vernonia arborescens* (L.) Sw. In describing *Conyza arborescens*, Linnaeus had before him not only the plate of Plumier, portraying the *Vernonia* of the Lesser Antilles, but also an actual specimen of a different species from Jamaica. A comparison of his text with the plate shows that the description could not have been taken from the plate alone, but was based primarily on the specimen. The latter accordingly becomes the type of the species and retains the specific name *arborescens*, and *V. icosantha* remains the first valid name for the species of Martinique and Guadeloupe.

Vernonia Shaferi sp. nov.

Stem shrubby, 1–2 m. high, the young branches closely cinereous-pubescent, becoming glabrate the second year; leaf-blades ovate-lanceolate or elliptic, the largest 4 × 12 cm., the upper much smaller, all acuminate, entire, acute at the base, dark green, minutely papillose-pubescent, and very sparsely resinous-dotted above, paler green but otherwise the same below; heads about eighteen-flowered, crowded in leafy secund cymes at the ends of the branches of the season; bracteal leaves oblong or oblong-ovate, acute, 5–10 mm. long; involucres broadly turbinate to campanulate, 6 mm. high, the scales rather closely imbricate, erect or appressed, narrowly oblong-lanceolate, acuminate, irregularly pubescent and ciliate, and usually resinous toward the

tip; achenes hirsute; pappus white, its bristles 6.5–7 mm. long, the paleae very irregular in length, as much as 1.5–2 mm. long, minutely erect-ciliate; flowers white or pink.

TYPE: *Shafer 172*, collected in Montserrat, January 23, 1907, and deposited in the herbarium of the New York Botanical Garden. The same herbarium also contains sheets of three other collections made on the same expedition, *Shafer 589*, *659*, and *661*.

This handsome species is obviously closely related to *V. longifolia* Pers., as shown by the shape and pubescence of the leaves, the inflorescence, and the character of the involucral scales. It is distinguished from that species at sight by the white pappus, as well as by the slightly larger heads, the much larger pappus-bristles, which are only 4–5 mm. long in *V. longifolia*, and the unusually long, barely ciliate paleae. It is a pleasure to name the species in honor of its first collector, the late John A. Shafer, who discovered several other interesting *Vernoniae* in the West Indies.

VERNONIA RACEMOSA Delp.

Vernonia racemosa Delp. Mem. Accad. Torino II. **14**: 396. 1854.

Vernonia arantpensis Gleason (in part), Bull. N. Y. Bot. Gard. **4**: 181. 1906, not Gardn.

Vernonia sericea L. C. Rich. subsp. *racemosa* Ekman, Ark. Bot. **13**$^{\mathrm{1b}}$: 85. 1914.

The two sheets in the herbarium of the New York Botanical Garden, which were referred by Ekman to *V. racemosa* as a subspecies of *V. sericea*, differ in certain features from *V. sericea*, with which they are not associated geographically, and agree better in general character with the linear-leaved species of Hispaniola and adjacent Cuba. The species-group *Arborescentes*, which includes *V. sericea*, has leaves of a broad type, not revolute, and comparatively few spreading cymes near the ends of the branches, producing a rather short and broad inflorescence. *V. racemosa* and its allied species have revolute, linear leaves and narrow, elongate inflorescences, composed of relatively short and few-headed cymes distributed over a considerable length of the axis. While this latter character is largely one of habit, the narrow revolute leaves afford a ready and accurate means of distinguishing it and its allies from the *Arborescentes*.

VERNONIA RIGIDA Sw.

Collected originally by Swartz in Jamaica in the middle of the eighteenth century, this excellent species has since been practically lost. Few botanists have examined Swartz's originals and as a result the name *V. rigida* has been applied by various collectors and students to several entirely different species. The genuine *V. rigida* was finally rediscovered by Wm. Harris at Upper Clarendon, Jamaica, December 27, 1917, and good specimens are now deposited in the herbaria of the Field Columbian Museum and the New York Botanical Garden. The species is obviously allied with the well-known Jamaican *V. acuminata* Less.

Vernonia Sagraeana angusticeps (Ekman) var. nov.

Vernonia angusticeps Ekman, Ark. Bot. 13^{15}: 14. 1914.

The sheet of *Wright 284*, on which the species of Ekman was based, in the Gray Herbarium agrees with the species in every particular except the small number (twelve) of flowers in the head and the consequently more nearly cylindrical involucre.

SPECIES-GROUP BUXIFOLIAE

In the mountains of Haiti and Santo Domingo occurs a group of three poorly known species of *Vernonia*. Only eight specimens have been examined in American herbaria by the writer, while Ekman mentions twelve in various European collections. One of these, the last to be described, is *V. Tuerckheimii* Urban, which seems to a well-marked and easily recognized species. Another is a form with small leaves, averaging only 7 × 12 mm., and a short, cylindrical or ellipsoid involucre 3–4 mm. in diameter, or spreading under pressure to 5 mm. For convenience this will be designated here as species A. The third, here referred to as species B, has leaves averaging 10 × 23 mm., and a turbinate or almost salviform involucre, spreading at its mouth to a width of 7–9 mm. even when not pressed. While the involucre of species A offers no noteworthy feature, that of species B is remarkable for its imbrication. It is composed of five vertical but gently spiral rows of scales, with ten to thirteen scales in each row, beautifully imbricated, and with the outer ones gradually reduced at the acuminate base of the head. Ekman had before him apparently

only species A; at least he cites two collections which cover that species in the New York collection and fails to mention the peculiar involucre of species B, which is utterly unlike that of any other North American species. This species A is designated by him *V. buxifolia* (Cass.) Less., although he has not seen Cassini's type, and as a synonym he adds *V. domingensis* (Spreng.) DC., the type of which he has seen. These two names have been regarded as synonymous for over eighty years. The writer, in 1906, considered that species B was the true *V. buxifolia*, and described species A as new under the name *V. montana*. From this description and the cited specimen Ekman recognized that *V. montana* was co-specific with the plants which he had examined, and reduced *V. montana* to synonymy. At the same time he was unable to match Gleason's description of *V. buxifolia* (species B) with anything he had seen in European collections and decided that it was probably a new species. When he examined the New York material of these in 1914 he annotated the sheets of species A as genuine *V. buxifolia* and those of species B as "*V. buxifolia* forma."

Cassini described the involucre of *Lepidaploa buxifolia* as turbinate and regularly imbricated, with an assemblage of short rounded scales covering the summit of the peduncle at the base of the head. In this feature it can agree only with species B. De Candolle, in examining the type of Sprengel's *Proustia domingensis*, used terms which certainly apply to species B, but which do not emphasize the peculiar involucre. One can scarcely imagine that he would have passed by such a striking feature if the specimen had exhibited it. The writer is therefore convinced of the justice of maintaining *V. buxifolia* for species B, as he did in his revision in 1906. For species A, he must be guided by the negative evidence of De Candolle and the positive statement of Ekman in regard to *V. domingensis*, use that name for species A, and relegate his own *V. montana* to synonymy.

Vernonia morelana sp. nov.

A shrub 3–5 m. high, branching above; stems striate, closely gray-tomentose, becoming glabrate with age; leaf-blade firm, dull-green, ovate-oblong, 3 × 7.5 cm., on tomentose petioles 8mm.

long, entire or with a few low teeth, obtuse or rounded at the base and apex, closely scabrous-pubescent above, finely gray-tomentose beneath; upper and rameal leaves similar but smaller and more densely tomentose, those in the cymes broadly ovate to subrotund, 5–15 mm. long; cymes freely branching, forming a hemispheric cluster 2 dm. wide at the end of the branches; heads 21-flowered; involucre campanulate, 4–4.5 mm. high, its scales regularly imbricate, all appressed or barely spreading at the tip, outer and middle scales ovate to ovate-oblong, sharply acute or cuspidate, tomentose-ciliate and often puberulent on the back, inner scales lanceolate, sharply acute or subacuminate, 4 mm. long, nearly or quite glabrous; achenes thinly pubescent and densely resinous-glandular; pappus white or very pale tawny, the bristles 6 mm. long, the paleae narrow, 0.6–0.8 mm. long.

TYPE: *Pringle 7697*, collected by streams, Cuernavaca, Morelos, Mexico, altitude 5,000 feet, March 16, 1899, and deposited in the herbarium of the New York Botanical Garden.

While this species clearly resembles the other members of the species-group *Deppeanae* in leaf-habit, inflorescence, and pubescence, it is distinct in its glandular achene, a structure not observed elsewhere in the group. It resembles *V. canescens* H.B.K. in its white pappus, but differs in its pubescence and broader involucral scales. It approaches *V. Deppeana* Less. in its leaf-pubescence, but differs in its white pappus, sharper scales, larger involucre, and broader paleae. It is even more widely separated from the other species of the group.

Vernonia salamana sp. nov.

A shrub, 2–2.5 m. high, branching above; stem striate, thinly cinereous-pubescent or becoming glabrate; leaves thin but firm, pale olivaceous, the blades ovate-elliptic, 3 × 7 cm., undulate, entire or remotely denticulate with low teeth, obtuse or subacute, obtuse or rounded at base, distinctly pubescent or subtomentose above, finely pubescent beneath, especially on the prominent reticulated veins; petioles 4–8 mm. long, or the upper leaves nearly sessile; inflorescence of freely branched cymes, terminating the stem and the upper axillary branches and forming a large pyramidal panicle 2.5 dm. in diameter; rameal leaves similar to the cauline but smaller; cyme-branches leafless, straight, bearing three to six sessile, secund, 21-flowered heads; involucre broadly campanulate, 4–5 mm. high, its scales loosely but regularly imbricate, pale green with a darker spot near the tip, ciliate, puberu-

lent on the back, obtuse to broadly rounded at the tip, the mid-vein becoming prominent near the apex and usually prolonged into a minute mucro; achene minutely pubescent on the ridges; pappus pale tawny, its bristles 4 mm. long, the paleae narrowly linear, about 0.4 mm. long.

TYPE: *Maxon & Hay 3385*, collected on dry plains near Salamá, Guatemala, January 22, 1905, and deposited in the herbarium of the New York Botanical Garden.

Vernonia salamana apparently finds its nearest relative in the well-known *V. patens* H.B.K., with which it agrees in its achenes, pappus, involucral scales, olivaceous leaves, and the finely pubescent lower leaf-surface. The shape of the leaf-blade is unlike that of *V. patens* and is closer to that of *V. Deppeana* Less. The pubescence on the upper side of the leaf and the prominent venation are distinctive.

VERNONIA MOLLIS H.B.K.

A plant collected by the Brothers Seler, number *3371*, has been identified by Hieronymus as *V. mollis* H.B.K. and distributed to American herbaria under that name. Ekman has considered the specimen as *V. canescens* H.B.K., to which it is obviously closely related, but from which it differs in the flat leaves and the tomentose lower leaf-surface, in its involucral scales, which are all subulate, and in its general habit. At the same time, it is doubtful if it is the true *V. mollis*. This is a Colombian species, described as having leaves sericeo-lanuginous beneath. This character is met with in certain Colombian specimens in the New York collections.

Vernonia ctenophora sp. nov.

Stem herbaceous, at least 4 dm. high, finely striate, thinly pubescent and resinous-dotted; leaves sessile or with petioles 2–4 mm. long; leaf-blades thin, ovate-lanceolate, entire, acuminate, obtuse or rounded at the base, as much as 5 cm. long by 2 cm. wide or the upper somewhat smaller, thinly puberulent and conspicuously glandular-dotted above, closely and finely gray-pubescent and resinous on the surface beneath and sparsely pubescent on the midrib and the obscure lateral veins; inflorescence of two or three elongated, erect, terminal or subterminal cymes; bracteal leaves resembling the cauline and progressively smaller, the upper only 15–20 mm. long; heads 20–35 mm. apart, sessile, 18–21-flowered; involucre campanulate,

6–7 mm. high, its scales irregularly but rather closely imbricate, the outer and middle with triangular-ovate or oblong appressed bases and long subulate tips, the inner linear-oblong, rather abruptly acuminate and most of them subulate-tipped, and all thinly pubescent with dark-colored hairs and sparsely resinous; achenes thinly pubescent, sharply ribbed, 1.5 mm. long; pappus white, its bristles 4 mm. long, prominently barbellate, the paleae little wider than the bristles, 0.6 mm. long, sharply ciliate with salient teeth.

TYPE: *E. A. Goldman 508*, collected at Apazota, Campeche, Mexico, December 30, 1900, and deposited in the United States National Herbarium as sheet 396871.

Vernonia ctenophora is a member of the species-group *Argyropappae*, as indicated by the resinous-dotted leaves and the long subulate involucral scales. Within the group it is most closely related to *V. hirsutivena* Gleason, from which it is distinguished by the conspicuously barbellate pappus bristles, the sharply ciliate and shorter paleae, the thinly pubescent involucre and achenes, the comparatively thin pubescence on the veins, and the numerous resin-dots on the upper surface of the leaf.

VERNONIA MISSURICA Raf.

Vernonia illinoensis Gleason, Bull. N. Y. Bot. Gard. 4: 211. 1906.

Throughout its wide range, which is more extensive and covers more diverse environmental conditions than that of any other species in the United States, *V. missurica* exhibits a considerable variation in structure. This variation pertains chiefly to the inflorescence and leaf-pubescence and less to the characters of involucre and achene.

Judged from herbarium evidence and field experience, the species is best developed in Indiana, Illinois, and northern Missouri, where it is by all odds the most common species of the genus. Here the inflorescence is broad, freely branched, with many heads, and relatively flat, and the leaves are thinly but closely tomentose beneath with cinereous multilocular hairs which cover the surface and veins alike. Farther to the northeast, at the border of its range in Michigan and Ontario, the multilocular hairs on the leaf-surface are relatively fewer and usually

replaced by short straight conical hairs. The leaves are smaller and proportionately narrower, and frequently with a basal taper. Because of these structures, the species is frequently mistaken for *V. altissima* Nutt., from which it may be distinguished by the resin-dots on the leaf, involucral scales, and achenes. This extreme form has been described by Daniels under the name *V. michiganensis*, and the same thing from Ontario appears in several herbaria under another unpublished name.

Throughout this whole region, from Michigan to Missouri, the plants exhibit generally rounded to subacute, purple involucral scales, imbricate in relatively few series, and a purple pappus. This is the form described by the writer as *V. illinoensis*.

West of this region the species is much less common, and the herbarium material has been collected in widely scattered localities as far south as southern Texas. In general, the collections from west of the Mississippi and south of the Missouri Rivers have a loose open inflorescence, sharper and frequently smaller involucral scales, imbricate in relatively many series, and frequently green instead of purple, and a pappus which soon becomes tawny in color when exposed to light. But these differences are not constant nor even coincident on the same plant, so that even well-marked varieties can not be accurately distinguished. Yet in four cases out of five the geographical origin can be correctly guessed merely by a glance at the involucre of the plant.

Another area in which a form of the species occurs is the coastal region of southern Mississippi and Alabama. Whether similar plants also occur in southern Louisiana and southeastern Texas is not known definitely, but the inference is that they do. This extreme southeastern form differs in certain features from the species, so that it is recognizable at a glance, and it may be described as a variety.

Vernonia missurica austroriparia var. nov.

Inflorescence more or less elongate, very loose, open, irregular, and few-headed; leaf-blades broadest distinctly above the middle, thinly tomentose beneath or merely pubescent; resinous glands on the leaves, scales, and achenes as in the typical form of the species.

TYPE: *Tracy 8015*, collected at Tensaw, Alabama, August 18, 1904, and deposited in the herbarium of the New York Botanical Garden. Other specimens are: *Tracy 6970* from Ocean Springs, Mississippi; *Tracy 4780* from Coopolis, Mississippi; and various specimens collected by Mohr at or near Mobile, Alabama. In some specimens the leaf-pubescence is reduced in amount until the leaf resembles that of *V. altissima*. Such plants have been included under this variety because of the size of the heads, the character of the involucre and inflorescence, and the presence of resin.

Vernonia aborigina sp. nov.

Stem herbaceous, stout, striate or ribbed, covered with a brown tomentum becoming thicker above; leaf-blades ovate-lanceolate, remotely denticulate with low ascending callous teeth, acuminate, narrowed below into an obtuse or rounded sessile or subsessile base, 8–15 cm. long, scabrous above with short papillose hairs, densely brown-tomentose beneath; inflorescence rather small and compact, 11–13 cm. wide and bearing relatively few (about 30) heads; bracteal leaves on the cyme-branches lance-oblong, 10–15 mm. long; heads large, in fruit about 12 mm. high, containing in the single head counted 68 flowers; involucre broadly rounded at the base, 7–8 mm. high, expanding to 16–18 mm. wide at maturity; involucral scales closely and regularly imbricated, the outer minute and triangular and all squarrose or recurved at the tip, acute, sparingly ciliate along the brown margin, resinous-glandular and thinly puberulent along the purple central two thirds, elsewhere green and glabrous, tipped with a rather prominent carinate midvein which is frequently prolonged into a short mucro; achenes 3.5 mm. long, olive in color, with low ridges and broad flat furrows, conspicuously glandular in the furrows, minutely and sparsely puberulent on the ridges; pappus-bristles reddish-tawny, almost plumose below, merely barbellate above, 7 mm. long, paleae as long as the diameter of the achene, narrowly linear, equaling in width or barely wider than the bristles.

The type was collected by P. H. Rolfs in Oklahoma, west of Fort Smith, Arkansas, August, 1891, and is deposited in the herbarium of Iowa Agricultural College as sheet number 32272. No other material has been examined.

The description of this new species is offered with considerable reluctance, because of the great variabilty of the western species and their known tendency to hybridize. In several features it differs from all other western species. The large heads, the un-

usual number of flowers in each head, the olive-colored, glandular achenes, and the reddish, conspicuously barbellate pappus distinguish it from all others. The squarrose scales separate it from all others except *V. Baldwini* Torr., the very narrow paleae from all except *V. interior* Small and the species-group *Fasciculatae.* It is to be hoped that further collecting in a somewhat neglected region may bring to light additional material.

Vernonia fasciculata nebraskensis var. nov.

Leaves shorter than in the typical form of the species, narrowly lanceolate, denticulate, acute, pale-green or yellowish green; heads closely crowded.

TYPE: *Rydberg 5400*, collected in Kearney County, Nebraska, July 14, 1900, and deposited in the herbarium of the New York Botanical Garden. Numerous other sheets occur in all larger herbaria; in fact, almost all of the Nebraska specimens labeled *V. fasciculata* are to be referred to this variety. The species proper occurs only along the Missouri River, so far as known to the writer, while the variety extends westward more than half the length of the state. Although the brief varietal description apparently offers but little evidence for the separation of a variety, nevertheless the Nebraska specimens in any large herbaria all look alike, all look different from the rest of the species, and can be separated at a glance even by a person not familiar with the genus, as the writer has been able to demonstrate.

VERNONIA ALTISSIMA PUBESCENS (Morris) Daniels

Inner involucral scales tipped with a short, straight, flat, erect, linear tip, not over 2 mm. long.

While Morris's variety was originally separated primarily by the character of the foliage, this is, as has been pointed out by Blake, due to some unusual pathological or teratological condition. The shape of the scales, on the other hand, is found as described above not only in Morris's type but in several other herbarium sheets from the Alleghenian region, from Pennsylvania and Ohio south to Alabama and South Carolina, and in isolated collections of Wilkinson from Mansfield, Ohio.

Vernonia altissima brevipappa var. nov.

Lower surface of the leaf-blades with a few multilocular hairs along the veins; paleae only 0.1–0.3 mm. long; otherwise as in the typical form of the species.

TYPE: collected by J. Schneck at Mt. Carmel, Illinois, August 13, 1891, and deposited in the herbarium of the University of Illinois.

Vernonia altissima laxa var. nov.

Heads smaller than in the species, 13–21-flowered; inflorescence broad, irregular, very loose and open; inner involucral scales often apiculate, the middle scales frequently sharply acute; resin-dots none; leaf and pubescence as in the typical form of the species.

TYPE: *Harper 1936*, collected at Newton, Georgia, August 19, 1903, and deposited in the herbarium of the New York Botanical Garden; duplicates of the type are in the Gray Herbarium and the herbarium of the Field Columbian Museum. Other specimens of this southern or coastal plain variety are *Tracy 8046* and *Eggleston 5142*.

Vernonia flaccidifolia angustifolia var. nov.

Leaves narrowly lanceolate, denticulate, only 1–2 cm. wide; otherwise as in the typical form of the species.

TYPE: *ex herb. Torrey*, collected in Alabama and deposited in the herbarium of Columbia University; another sheet in the New York collections is from Georgia, ex herb. Chapman.

Vernonia ovalifolia purpurea var. nov.

Leaves with numerous multilocular hairs on the veins of the lower surface, the upper leaves subtending the branches truncate on rounded at the sessile base; pappus purple; otherwise as in the typical form of the species.

TYPE: *F. S. & E. S. Earle 99*, collected at Auburn, Alabama, July 22, 1899, and deposited in the herbarium of the New York Botanical Garden.

Vernonia jucunda sp. nov.

Stem apparently herbaceous, at least 4 dm. high, erect, sparingly branched, densely villous when young, becoming floccose when older and glabrate at about 3 dm. from the summit, faintly

striate and reddish brown under the pubescence; leaf-blades ovate-oblong, as much as 38 × 80 mm., narrowed toward the sessile base or into a short margined petiole, undulate and irregular at the entire margin or rarely with a few low salient teeth, frequently a little revolute, acute at the apex or short-acuminate into a small subulate tip, dark-green and rugose above with impressed veins and scabrous with papillose hairs or hair-bases, gray or nearly white beneath with a close fine tomentum; lateral veins prominent, ascending and straight almost to the leaf-margin; upper and bracteal leaves similar but smaller; heads five-flowered, in a sympodial raceme, standing opposite and a little (2–3 mm.) below a bracteal leaf which later bears secondary heads in its axil, primary heads eight to ten; involucre 8 mm. high, 2.5 mm. wide, with its stiff scales imbricate and appressed at the base and squarrose at the tip, lanceolate-oblong to ovate-oblong, broadest below or near the middle and long-acuminate into a subulate, glabrous, terete, callous tip, the outermost green, one-half the length of the purple inner ones, and all papillose-villous with erect hairs on the exposed portion; corolla apparently pale purple, its tube glabrous, not ampliate above, 5 mm. long, its lobes glabrous, 3 mm. long by 0.6 mm. wide, with parallel sides and triangular tip; filaments glabrous, attached at two thirds the height of the tube; anthers 2.8 mm. long, minutely rounded at the triangular tip, their obtuse bases 0.5 mm. long; style hairy along the upper 1.4 mm., its branches 1.4 mm. long, tapering, hairy on the outer side; achene 2.5 mm. long, shallowly ten-ribbed, pubescent with short erect hairs on the ridges; pappus-bristles pale tawny, 6.5 mm. long, barbellate; paleae linear-lanceolate, 1.0–1.1 mm. long by 0.09–0.18 mm. wide, trough-shaped and pubescent on the inner face.

TYPE: *Purpus 7060*, collected in the Sierra de Tonala of Chiapas, Mexico, October, 1913, and deposited in the herbarium of the University of California as number 173434. Other sheets of the same collection are in other American herbaria and agree in every particular with the type.

Vernonia jucunda is the first species of the section *Stenocephalum* to be discovered in North America. Other members of the section are South American; one species, probably undescribed, occurs in Colombia and a number in Brazil. The section is characterized by few-flowered heads set a short distance below the bracteal leaf, by an involucre constricted at the throat and composed of subulate, more or less squarrose scales, and by leaves which are usually revolute and tomentose beneath.

Among the many interesting plants collected by Charles Wright in Cuba, his number 2789, described by Grisebach as *Vernonia lepidota*, is one of the least known. Wright described it as a suffruticose plant, ascending on bushes to a height of about 3 meters, with purple flowers. The Gray Herbarium contains a large specimen which shows the foliar characters very well, but is too immature for a careful study of the floral structures, achenes, or pappus. Ekman examined three sheets of the same number in European herbaria, including Grisebach's type, and has published the first good description of its reproductive structures. A few of his observations have been verified at the Gray Herbarium. Ekman points out that its anthers and styles agree with those of the genus *Vernonia*, but that its pappus is entirely different. The inner pappus is composed of not more than seven flattened bristles, and the outer of scales which are coalescent into a cylindrical tube with lacerose margin. This feature alone is sufficient to warrant the erection of a genus for it, which may appropriately be named in Ekman's honor.

EKMANIA gen. nov.

Inflorescence a corymbiform cluster, freely branched and beset with petiolate bract-like leaves; heads homogamous, few-flowered; involucre of a few series of closely appressed scales; corolla glandular without; style and anthers as in *Vernonia*; achene glabrous, ten-ribbed; pappus biseriate, the outer of a cylindrical tube with lacerose margin, the inner of five to seven stout flattened bristles; stem and foliage lepidote.

Type species: *Vernonia lepidota* Griseb.

Ekmania lepidota (Griseb.) comb. nov.

Vernonia lepidota Griseb. Cat. Pl. Cub. 145. 1866.

Leaf-blades elliptic-oblong, the larger ones 3.5 × 8 cm., the upper smaller, thinly silvery-lepidote above, densely fulvous-lepidote beneath, entire, obtuse or subacute, prominently veined; the larger bracteal leaves petiolate, 10–13 mm. long and one-nerved, the others more crowded distally and gradually reduced in size to short subterete scales 2 mm. long, closely appressed to the involucre and distinguished from it chiefly by their lepidote pubescence; involucre 3 mm. high, its brown scales trough-shaped or boat-shaped, acute, pubescent or scurfy on the back.

Oliganthes Milleri (Johnston) comb. nov.

Vernonia Milleri Johnston, Proc. Am. Acad. 11: 698. 1905.

The structure of the pappus of this little-known species from the island of Margarita indicates clearly its affinity with *Oliganthes* rather than with *Vernonia*.

Piptocoma rufescens latifolia var. nov.

Leaf-blade narrowly ovate or elliptic, two to three times as long as wide, broadly obtuse or rounded at the apex, abruptly narrowed at the base, its tomentum loose and thin; petiole 1 cm. long; involucre larger and its scales more tomentose than in the typical form of the species.

TYPE: *Britton, Britton & Shafer 104*, from a coastal thicket on Water Island, St. Thomas, January 31 to February 4, 1913, and deposited in the herbarium of the New York Botanical Garden; a second sheet in the same collection is *Britton & Shafer 845*, from a coastal thicket on Salt Island, Tortola.

The species of *Elephantopus* occurring in the southeastern United States have long been a difficult problem for taxonomists. *E. carolinianus* Willd. and *E. nudatus* Gray are quite distinct and have generally been recognized. Gray, in the Synoptical Flora, in 1886, combined *E. tomentosus* L. with *E. elatus* Bertol., and in general Bertolini's species was not recognized until 1901. Baker then regarded it as distinct and gave some valuable comparative measurements. While the difference in length of involucral scales and pappus is distinct in mature heads, it is not always reliable at earlier stages. Possibly for this reason, Baker's measurements have been neglected by recent authors, and Small has separated the two species chiefly on characters of leaf and pubescence, which are unfortunately exceedingly variable.

One diagnostic character has however been overlooked. In *E. tomentosus* the hairs on the midvein are generally reflexed, while on the leaf-surface proper many or all of the hairs point backward. In *E. elatus* the hairs of the midvein are longer and stiffer and point distinctly forward. Separated by this character, many specimens usually referred to *E. tomentosus* are found to belong to the other species, having also the short, heavily invested scales

and short pappus ascribed by Baker to *E. elatus*, and only the leaf-shape of *E. tomentosus*. These may be described as a variety.

Elephantopus elatus intermedius var. nov.

Leaf-blade elliptic or oblong, abruptly narrowed to the base, less than three times as long as wide; stem comparatively short and sparingly branched; pappus sometimes as much as 5 mm. long.

TYPE: *Tracy 4741*, collected at Coopolis, Mississippi, September 8, 1898, and deposited in the herbarium of the New York Botanical Garden. The variety is represented in herbaria by numerous specimens, and is distributed from southern Mississippi east along the coastal plain to Georgia and south to Lee and Dade Counties in southern Florida.

NEW YORK BOTANICAL GARDEN

Storied or tier-like structure of certain dicotyledonous woods*

Samuel J. Record

A considerable number of dicotyledonous woods are characterized by a storied or tier-like arrangement of their secondary elements. Such woods exhibit on longitudinal section, typically on the tangential, fine transverse lines, bands or striations commonly called "ripple marks." These markings may be distinct to the unaided eye, may be at or near the limit of vision, or may require the lens. In some cases they may be more readily seen without the lens than with it, or they may be fairly distinct under the lens but indistinct or apparently absent under the compound microscope. In specimens with very dark and infiltrated heartwood the markings may be obscured there but show plainly in the sapwood; usually, though, they appear to best advantage in the heartwood.

In woods with this type of structure the cambial cells are in tangential as well as radial seriation and part or all of the elements to which they give rise preserve this arrangement. Ordinarily it is only in stems of considerable thickness that the tiers assume a marked regularity, but the diameter a stem must attain before the storied structure becomes pronounced is subject to wide variation, depending not only on the species but also on the rate of growth. In certain stems of Leguminosae and Zygophyllaceae the tiers were found to be fairly regular in what was apparently the second annual ring, less than one eighth inch from the pith. In general, though, this feature is wanting in the twigs of herbarium material.

The storied structure may not extend to all of the elements. In the extreme and also the most common form (Zygophyllaceae, Bignoniaceae, Leguminosae in large part, and others) the rays, vessel segments, tracheids, wood fibers, and wood parenchyma strands are all in horizontal seriation. On the tangential surface the cross sections of the rays appear as short, closely spaced, par-

* Contribution from the Yale School of Forestry, No. 4.

allel lines, often of very regular length and arrangement, while separating the tiers is a fine line of lighter or darker shade than the remainder of the wood. These lines are made by the junctions of the tiers of wood cells and vary in appearance according to the elements involved in a particular area, whether fibers with interlacing tips or vessel segments and wood parenchyma cells with abrupt terminations. In some instances, also, the local aggregations of pits in the fiber walls where the lumina become constricted tend to increase the refraction there and make the lines more distinct. According to Von Höhnel (1, p. 33) this is very pronounced in *Bocoa provacensis* Aubl. (*Inocarpus edulis* Forst.); his findings are confirmed by Wiesner (5, pp. 15, 950), who figures the pits. In the cases investigated by the present writer such pit-areas were noted in several woods, as for example, in *Machaerium*, *Physocalymma*(?), and *Erythrina*.

Where the rays are all storied they occupy the median portion of each tier, the height of which is usually considerably greater than the height of the rays. Consequently there is room for considerable variation in the height of the rays without interrupting the regularity of the transverse markings. It is not uncommon to find some of the rays grown together at the margins and thus occupying two or three stories, as for example, in *Cercis*, *Crescentia*, *Ormosia* and *Ougenia*. Where the rays are in perfect seriation, a section between two tiers misses them completely. In most instances, however, such a section shows rayless gaps, the width of which depends upon the regularity of stories.

In some storied woods, especially in the Bombacaceae, Malvaceae and Sterculiaceae, the rays are of two general sorts, large and small. Here only the low rays are in seriation and they may be so few, comparatively, and so over-shadowed by the large rays that the "ripple marks" are indistinct except in proper light and may be easily overlooked in casual inspection. In some of these woods the markings may be plainer without the lens than with it and, because of the very limited field under observation, may not be distinguishable at all under the compound microscope.

In both of these types the elements other than the rays are normally storied. The vessel segments and vascular tracheids correspond in length to the height of each tier, though occasional

short segments are found which appear to be subdivisions. The wood parenchyma strands show a uniformity in length with the vessel segments, but in a few cases where parenchyma is scanty the vessel segments and tracheids (when present) seem to be entirely responsible for the "ripple marks." This was found to be the case in *Dalea spinosa* Gray, *Artemisia tridentata* Nutt., and *Bigelovia graveolens* Gray.

The number of parenchyma cells per strand is not constant but in most of the woods investigated was found to be two or four; sometimes only one (an intermediate or substitute fiber). It is not uncommon to find that the metatracheal strands are composed of two cells and the paratracheal of four. Where the parenchyma is abundant, the component cells of the strands may be uniformly disposed and thus give rise to a secondary seriation which, especially if the cells are large, is readily visible under the lens. In this case the height of the tiers in only one half or one fourth that of the ordinary tiers. In species of *Bombax*, *Ceiba* (*Eriodendron*) and *Heliocarpus* the number of cells per strand is four; in *Charpentiera*, *Diphysa* and *Lonchocarpus*, two; in *Gossypium* and *Pterocymbium*, two in the metatracheal and four in the paratracheal. The same structure obtains in some of the finer-textured woods, but the small size of the cells usually renders it indistinct or invisible under the lens. It was found fairly distinct in *Ichthyomethia piscipula* (L.) Kuntze (mostly two cells per strand) and less so in *Tabebuia Guayacan* Hemsl. (four cells per strand).

The libriform fibers and fiber-tracheids (collectively, wood fibers) may or may not show distinct seriation in the tangential section. In all ordinary cases the fibers are much longer than the vessel segments or the height of the tiers. In many cases there is a widened middle portion equal to about one third of the total length of the fiber and corresponding to the length of the original cambial cell. The attenuated ends of the fibers of one tier are forced during elongation between the fibers of the tiers immediately above and below and, in consequence, a cross section through the middle portion of a tier will show (under the compound microscope) alternate rows of large and small cells, the latter being twice as many as the large ones. A section through the junction of two tiers will show fewer cells and they will be more nearly uniform

in size. In many woods the fibers show a gradual instead of abrupt diminution in caliber and the feature just mentioned is absent or indistinct. It may require careful maceration to determine whether or not the fibers are storied, particularly in woods with irregular rays. The fact that the fibers are so interlaced and dove-tailed together prevents woods with storied structure from being weakened or made brittle thereby.

In *Herminierā elaphroxylon* Guill. & Perr., the wood cells ("palisade tracheids" of Jaensch, 3, p. 269) are parenchymatous and arranged in regular stories. Some of the cells are subdivided but not very regularly. The low uniseriate rays are storied while the large ones (which may contain vessels) are not. The vessel segments are mostly of the same length as the height of the tiers but according to Wiesner (5, p. 20) some of them may be subdivided. The wood fibers, which are distributed in narrow layers, are three times the length of the other elements and have localized pit areas at the constrictions. Solereder (6, p. 276) figures *Aeschynomene* sp. with the parenchymatous wood cells much pitted at the ends. The present writer did not have opportunity to study woods of this genus but found much the same structure in *Erythrina* spp., except that all or nearly all of the rays are large and the wood fibers in the scattered bands are apparently not storied. The parenchymatous cells making up the ground mass are large, thin-walled, blunt-ended, and usually subdivided into two cells about the vessels. The markings vary from distinct in some specimens to barely visible without lens in others.

Where the elements of the wood are definitely storied it is, of course, to be expected that the same arrangement will likewise appear in the secondary phloem. In the limited number of stems with bark examined by the writer this was found to be the case and in some instances, *Dalea spinosa* for example, the feature was more distinct on the inner surface of the bark than in the wood. An unusual case was found in *Olneya tesota* Gray, where the inner surface of the bark exhibits, under the lens, fine but distinct and fairly regular cross-lines (150–160 per inch) without, apparently, any corresponding structure in the wood. Under the compound microscope the vessel segments and wood parenchyma strands are indistinctly storied, but the rays and apparently the fibers are

not, while the vertical elements of the secondary phloem are in horizontal seriation. The distinctness of the cross-lines in the inner layers of phloem was found to be largely due to highly refractive callus on the sieve plates.

The storied structure of wood occurs throughout a considerable range of families and orders as will appear from the following list, which is arranged according to the Engler and Gilg (1912) system of classification. The first numeral following the family refers to the number of different genera in which the feature has been noted by the writer; that in parentheses, to the total number reported.

1. URTICALES: Ulmaceae, 1 (1); Moraceae, 1 (1).
2. CENTROSPERMAE: Amarantaceae, 1 (1).
3. RHOEADALES: Moringaceae (1).
4. ROSALES: Rosaceae (1?); Leguminosae, 40 (51).
5. GERANIALES: Zygophyllaceae, 3 (4); Rutaceae, 1 (1); Simarubaceae, 3 (4); Meliaceae, 6 (7).
6. SAPINDALES: Hippocastanaceae, 1 (1); Sapindaceae (1).
7. MALVALES: Tiliaceae, 5 (8); Malvaceae, 4 (4); Bombacaceae, 3 (3); Sterculiaceae, 7 (8).
8. MYRTIFLORAE: Lythraceae, 1? (1?).
9. EBENALES: Ebenaceae, 1 (1).
10. TUBIFLORAE: Bignoniaceae, 3 (3).
11. CAMPANULATAE: Compositae, 3 (3).

Consideration of the above list leads to the conclusion that there is no close correlation between the form of wood structure under consideration and the various types of floral organization which serve as the basis for the classification followed. There seems to be a correlation, however, between this storied structure and certain types of differentiation of the wood elements. The vessel segments have abrupt ends and simple perforations, and the elongated or scalariform type of pitting is rarely found and then only in the tracheidal vessels and vascular tracheids. The wood fibers are for the most part provided with simple pits or with pits having only small and indistinct borders. The pits between vessels and parenchyma are usually small and half-bordered. It is also interesting to note that with very few exceptions (notably *Aesculus*, *Cercis*, *Cytisus*, *Diospyros* and *Tilia*) the woods are of tropical or subtropical origin.

There is no family, with the possible exception of the Zygo-

phyllaceae (only a few woods of which were studied), in which all of the woods are characterized by horizontal ranking of their elements. In many cases it appears to be a generic character but more often it is specific only. A few instances have been noted where the feature is not constant for a given species and may be of only local occurrence in the same specimen. One of the best examples of this is furnished by *Swietenia*, where "ripple marks" exhibit wide variation in regularity and occurrence and are about as likely to be absent as present. In general, however, the constancy of the feature seems to bear a direct relation to the degree of regularity of the cross-markings. It is most dependable when all of the elements are involved and especially when the rays are fine and of uniform height.

In this investigation attention has been given to the elements storied, the regularity and visibility of the transverse markings and to the height of the tiers in each wood examined. In most instances only the gross and lens characters are given since they are most readily employed in practice. There are so many factors entering into the question of distinctness or visibility that the particular observations of the writer may not always apply. For instance, in *Guaiacum* the markings, though extremely fine, are distinct under the lens in the sapwood and may be indistinct or even invisible in very resinous heartwood. Usually the visibility is materially increased by moistening the surface, but in some instances the opposite effect is produced.

According to Von Höhnel (2, p. 2) the distance between the cross-lines varies from one half to one eleventh of a millimeter, and for a given species is constant. In order to determine whether or not there is a definite tier-height for each species the present writer counted the number of tiers per inch of length on the tangential section of every specimen examined. An inch, divided into quarters, was marked off and the count and recounts made under the lens for the entire inch, the quarter-marks serving as an additional check. In the larger specimens, at least two different inches were counted. In some instances the markings, being fairly distinct without a lens but indistinct with it, were counted with the naked eye or with the aid of a reading-glass. Where the rays are not in seriation the cross-lines are likely to be

indistinct, and the most satisfactory results can be secured by counting the vessel segments. In the Zygophyllaceae the lines, though very uniform and readily visible under the lens, are so very closely spaced (about 250 per inch) that is it practically impossible to make an accurate count without the use of the compound microscope. By using low power and reflected light the smooth surface of a small specimen can be readily examined and measurements made without preparing thin sections.

Considerable variation in tier-height was found not only in different specimens of the same species but also in the same specimen. Even within a given inch of length the number per quarter may show a variation of from two to five as a result of the occasional to frequent bifurcation of the tiers, with consequent narrowing at the point of branching. The greatest variation in tier height within a species was noted in *Diospyros virginiana* L., where the counts per inch on eleven different specimens were as follows: 57, 57, 58–60, 60, 61, 62, 63, 66–68, 70–72, 72–74, 81–82; a maximum difference of 25 per inch, or nearly 45 per cent on the basis of the minimum. In only one other case did the variation exceed 20 per cent, and almost always it was less than 10 per cent.

In 86 woods of the Leguminosae the number of markings per inch were as follows: under 100, 29 per cent; 100 up to 125, 34 per cent; 125 up to 150, 21 per cent; 150 to 190, 12 per cent. Nearly every wood showing between 125 and 190 "ripple marks" per inch belongs to the Leguminosae. The investigated woods of the Zygophyllaceae have considerably more than 200 per inch, mostly about 250, and may, by means of this feature alone, be readily separated from all of the others. This fact has proved of practical value in distinguishing the wood of true lignum-vitae from its various substitutes.

The present investigation fails to confirm certain findings of other writers. Von Höhnel (1, p. 38) states that the rays are storied in *Parkinsonia*, but there was no evidence of this in the specimens examined by the writer. The grenadillo wood is referred to as "*Inga vera* W.?" (p. 39) but this is probably incorrect, inasmuch as various specimens of *Inga* spp. were found to be without any tendency to storied structure. The name "grenadillo" is applied to several woods, one of which is *Brya Ebenus* DC. Another wood with "ripple marks" was provisionally identified

by the same author as *Conocarpus erecta* (Combretaceae), but authentic specimens of this species are wholly without this structure, as are all other representatives of the family that were examined. Wiesner (5, p. 997) states that in *Olea europea* L. the rays (under the lens) produce a fine wavy cross-striping on the tangential section. Specimens of the wood examined by the writer exhibit no tendency to "ripple marks," and Müller (Atlas der Holzstructur, 1888, pp. 88, 91) gives as one of the distinguishing features of this wood the irregularity in size of the rays. All of the foregoing woods are excluded from the table given below.

The only representative of the Lythraceae included in the list is *Physocalymma scaberrimum* Pohl, variously known as Brazilian tulip-wood, rose wood, "páo de rosa," "cego machada," "grão de porco" and "sebastião de arruda." Writers all seem to be in agreement in referring this wood to the species mentioned, but the specimens examined by the writer, which are evidently the same as those described by Wiesner (5, p. 975), appear to belong to the Leguminosae. They certainly do not resemble other available material of the Lythraceae.

Another wood of which there is some doubt is *Ferolia guyanensis* Aubl. (= *Parinarium* sp.) of the Rosaceae, mentioned by Von Höhnel (1, p. 43), who calls it "Ficatin- oder Königsholz." According to Stone (Timbers of Commerce, 1904, p. 101) this species supplies the wood from Guiana commonly known as "washiba" or bow-wood. Authentic specimens of washiba and bow-wood, collected by the Forestry Officer of British Guiana are *Tabebuia* spp. The tier height in the latter is about 0.25 mm., while according to Von Höhnel the height of the "Markstrahlstockwerke" in the wood of *Ferolia* is about 0.15 mm. If Von Höhnel's measurement refers only to the height of the rays the discrepancy disappears, since this agrees closely with the writer's observations. No other wood of the Rosaceae has been reported as having a tier-like structure.

The satinwood, *Chloroxylon Swietenia* DC., is listed with the Rutaceae (following Engler), rather than with the Meliaceae, because the wood so closely resembles those of the Rutaceae and has so little in common with the others. No other representative of the Rutaceae has been found with storied structure, while various representatives of the Meliaceae exhibit a more or less

pronounced tendency in this direction. It is interesting to note, however, that the number of tiers per inch in the latter woods (so far as known to the writer) is between 45 and 55, while in the satinwood it is about 80.

Most of the woods with "ripple marks" belong to the Leguminosae. Following is a list of woods examined by the writer in which the storied structure was not observed, though a few (marked with an asterisk) have been reported by other writers and are included in the list. Some of the more common synonyms are placed in parentheses. These woods are: *Adenanthera*, *Albizzia**, *Bowdichia* (?), *Browneopsis*, *Cassia**, *Cercidium*, *Cercidophyllum*, *Cladastris* (*Copaiba*), *Copaifera*, *Cynometra*, *Daniellia* (?), *Dimorphandra*, *Enterolobium*, *Erythrophloeum*, *Eysenhardtia*, *Gleditsia*, *Gymnocladus*, *Haematoxylon*, *Inga* (see page 259), *Intsia*, *Kingiodendron* (?), *Lysiloma*, *Mimosa*, *Pahudia*, *Parkia**, *Parkinsonia*, *Peltogyne*, *Peltophorum* (?), *Piptadenia*, *Pithecolobium*, *Prioria*, *Prosopis*, *Pterodon*, *Robinia*, *Sindora* (*Vouacapoua*), *Zygia* (?).

In this investigation all of the woods in the extensive collections of the Yale School of Forestry were gone over. Since many of these are from tropical regions, of which our botanical knowledge is far from complete, it is by no means certain that all of the specific identifications are correct, though special effort was made to eliminate errors or indicate the doubtful cases. A considerable number of woods, mostly belonging to the Leguminosae, have been omitted because their botanical status has not been determined. The following table is published with a view of calling attention to an important feature of wood structure and with the hope of stimulating further investigation in this direction. The writer will appreciate assistance in correcting and extending the data.

NOTES: Under "rays not storied" are included woods which may have some of the rays, the small ones, in horizontal seriation. "Wood parenchyma cells storied" refers to the secondary seriation produced by the individual cells of the wood parenchyma strands; not visible without lens. "Fiber pits storied" refers to the horizontal seriation of special pit areas on the wood fibers. Where not noted does not necessarily mean that the feature is absent, since not all of the woods were examined microscopically. "Number of tiers per inch" applies exclusively to measurements by the writer and is the basis for "tier-height." A dash indicates a tendency. Data from other writers are credited to them and are as nearly complete as their descriptions will permit.

TABLE OF WOODS WITH TIER-LIKE STRUCTURE, SHOWING THE ELEMENTS STORIED, THE REGULARITY AND VISIBILITY OF THE TRANSVERSE LINES ("RIPPLE MARKS"), AND MEASUREMENTS OF TIER-HEIGHT

Scientific name	Common name	Country	Elements storied				Regularity of lines				Visibility				Measurements	
			All elements	Rays not storied	Wood parenchyma cells storied	Fiber pits storied	Regular	Fairly regular	Irregular	Local occurrence	Distinct—fairly so	Barely visible	Lens required	Indistinct with lens	Tier-height in mm.	Number of tiers per inch
AMARANTACEAE																
CHARPENTIERA OVATA Gaudich.	Papala	Hawaii		X	X			X					X		0.22–0.23	110–115
BIGNONIACEAE																
CRESCENTIA CUCURBITINA L.	Black Calabash	Florida	X						X			X			0.22–0.23	110–115
" CUJETE L.	Calabash	Porto Rico	X						X			X			0.21–0.22	115–120
TABEBUIA DONNELL-SMITHII Rose	Prima vera	Central America	X					X		X		X			0.25	100
" GUAYACAN Hemsl.	Yellow guayacan	Panama	X		X		X				X				0.28	90– 92
" NODOSA Griseb.	Toro-ratai	Argentina	X					X				X			0.17–0.18	140–145
" PALMERI Rose	Amapa prieto	West coast Mexico	X				X					X			0.20	124
" PENTAPHYLLA Hemsl.	(Roble)	Panama	X					X			X				0.29	84
" SCHUMANNIANA Urb.	Roble colorado	Porto Rico	X						X		X				0.29–0.31	80– 85
" sp. (No. 58)	Roble	Honduras	X					X			X				0.26–0.28	90– 96
" sp. (No. 97)	"	"	X					X			X				0.30	84
" sp. (No. 378)	"	Colombia	X				X				X				0.32–0.33	76– 78
" sp. (No. 351)	Apamate	Venezuela	X					X			X				0.32	78
" sp.	Hackia	British Guiana	X				X				X				0.26	94– 96
" sp.	Washiba Bow-wood	"	X				X				X				0.24	102–103
TECOMA ARALIACEA DC.	Surinam Groenhart	"	X				X				X				0.33	74
" CHRYSANTHA DC.	Araguaney	Venezuela	X				X					X			0.21–0.22	115–120
" LEUCOXYLON Mart.	Roble	Porto Rico	X						X				X		0.24–0.25	100–105
" OBTUSATA DC. (*T. Ipe* Liais)	Lapacho	Argentina	X				X					X			0.21	120

TECOMA SPECIOSA DC (Hohnel, I, p 41)			×			×	×							0 25	
" STANS Juss		West Indies	×						×		×			0 21	120
" sp (No 930)	Lapacho	Argentina	×				×				×			0 22–0 23	112–115
" sp (No 1124)			×				×				×			0 24	105–107
" sp (market specimen)	Bethabara	?	×				×				×			0 28	90
" sp (2 specimens)		Brazil	×				×			×				0 25–0 26	95–100
BOMBACACEAE															
BOMBAX CYATHOPHORUM (Casar) K Schum (*Pachira cyathophora* Casar)	Imbirussi	Brazil		×	×			×		×			×	0 63–0 71	35– 40
BOMBAX INSIGNE Wall	Didu	Andamans		×	×			×		×			×	0 42–0 43	58– 60
" sp ? (No 503)	Tolu	Colombia	—	×				×		×				0 40	63
" sp ? (No 1570)	Majagua			×				×		×				0 42–0 45	55– 60
CEIBA PENTANDRA (L) Gartn (*Eriodendron anfractuosum* DC)	Ceiba	Cuba		×	×			×			×			0 42	70
CUMINGIA PHILIPPINENSIS Vidal	Gapas gapas	Philippine Islands	×				×			×				0 33	75
COMPOSITAE															
ARTEMISIA TRIDENTATA Nutt	Sage Brush	California		×				×				×		0 13 ±	200 ±
BACCHARIS SAROTHROIDES Gray				×				×			—	×		0 20–0 21	120–125
BIGELOVIA GRAVEOLENS Gray		Colorado		×				×				×	×	0 13 ±	200 ±
EBENACEAE															
DIOSPYROS VIRGINIANA L (11 specimens)	Persimmon	Eastern United States	×				×	—	×	×				0 30–0 44	57– 82
HIPPOCASTANACEAE															
AESCULUS OCTANDRA Marsh (*A flava* Ait)	Buckeye	Central United States	×					×	×	×			×	0 36–0 43	58– 68
LEGUMINOSAE															
ALBIZZIA PROCERA (Willd) Benth (*Acacia procera* Willd , Hohnel I p 38)		Tropical Asia	×											0 20	
AESCHYNOMENE sp (Solereder 6 p 275)	Solah	India		×		×		×							
ANDIRA ANTHELMINTHICA Benth (Hohnel I, p 35)		Brazil?	×				×							0 25	

TABLE OF WOODS WITH TIER-LIKE STRUCTURE, SHOWING THE ELEMENTS STORIED, THE REGULARITY AND VISIBILITY OF THE TRANSVERSE LINES ("RIPPLE MARKS"), AND MEASUREMENTS OF TIER-HEIGHT—*Continued*

Scientific name	Common name	Country	Elements storied				Regularity of lines				Visibility				Measurements	
			All elements	Rays not storied	Wood parenchyma cells storied	Fiber pits storied	Regular	Fairly regular	Irregular	Local occurrence	Distinct—fairly so	Barely visible	Lens required	Indistinct with lens	Tier-height in mm.	Number of tiers per inch
LEGUMINOSAE—*Continued*																
ANDIRA INERMIS H. B. K.	Yaba	Cuba	×			×		×				×			0.26	93– 96
" " (Wiesner, 5, p. 947)	Partridge Wood	Tropical America	×				×						×			
APULEIA PRAECOX Mart.	Ibira pere	Argentina	×				×				×				0.24–0.26	95–105
" "	" "	"	×				×				×				0.28–0.29	85– 90
" sp. (No. 2497)	Faviero	Brazil	×				×				×				0.26	95
ARTHROCARPUM GRACILE Balf. f. (Saupe, 4)																
BAPHIA NITIDA Lodd. (Wiesner, 5, p. 936)	Camwood	Tropical Africa	×				×						×			
BAUHINIA LIGULATA Pittier		Panama	×					×			×				0.22–0.23	110–115
" RETICULATA DC. (Höhnel, 1, p. 37)		Africa?	×				×									
BELAIRIA MUCRONATA Griseb.	Yamaquey	Cuba	×				×						×		0.13–0.14	180–190
" SPINOSA A. Rich.	"	"	×				×						×		0.14	175–180
BRYA EBENUS DC.	Green Ebony	West Indies	×				×						×		0.15–0.16	160–165
CAESALPINIA CORIARIA Willd.	Divi-divi	Curaçao	×				×				×	—			0.21–0.23	110–120
" "	"	"	×						—	×		×			0.18	136
" "	"	India	×				×				×				0.19–0.20	126–132
" EBANO Karst.	Pao ferro	Brazil	×				×				×				0.25–0.26	95–100
" ECHINATA Lam.	Brazil-wood	"	×						×			×			0.28	90
" MELANOCARPA Griseb.	Guayacan	Argentina	×				×					—	×		0.18–0.19	130–135
" " ?	"	"	×				×					×			0.17–0.18	140–145
" SAPPAN L.	Sappan-wood	Philippine Islands	×						×	×		×			0.26	95

CAESALPINIA TINCTORIA Domb. (Hôhnel, 1, p. 37)		West Indies?	×					×							0.33	
CASSIA FISTULA L. (Hohnel, 1, p. 37)		India?	×					×							0.17	
CASTANOSPERMUM AUSTRALE A. Cunn. & Fraser	Black Bean	Australia	×				×			×	×	×			0.31–0.33	75–80
CENTROLOBIUM PATINENSE Pittier	Amarillo de Guayaquil	Panama	×				×					×			0.23–0.24	105–110
" ROBUSTUM Mart.		Colombia	×				×					×			0.23	110
" sp. ? (ten specimens)	Arariba	Brazil	×				×					×			0.21–0.25	100–200
" sp. ?	Guayacan Jobo	South America	×												0.25	100
CERCIS CANADENSIS L.	Redbud	Central United States	×					×					×		0.16–0.17	150–160
" SILIQUASTRUM L. (Wiesner, 5, p. 930)	Judas Tree	Europe	×					×				×	×		0.20–0.24	
COUMAROUNA ODORATA Aubl.	Tonka Bean	British Guiana.	×				×				×				0.31	80
" PANAMENSIS Pittier		Panama	×				×				×				0 30	82
" sp.	Coumaru	Trinidad	×				×				×				0.28	90
DALBERGIA BROWNEI Schinz.		Florida	×					×				×			0.21	120
" HUPEANA Hance		China	×					×				×			0.18	135–140
" LATIFOLIA Roxb	Rosewood	India	×												0.16–0.17	150–160
" NIGRA Allem. (Hohnel, 1, p. 37)		Brazil?	×				×	×				×			0.20	
DALBERGIA RETUSA Hemsl.	Cocobola	Panama	×					×				×			0.18	138–140
" sp. ? (two specimens)	"	Honduras	×				×					×			0.18–0.19	132–140
" SISSOO Roxb.	Sissoo	India	×					×					×	×	0.16	155–158
DALEA SPINOSA Gray	Indigo Bark	Southwestern United States		×											0 17	150
DIALIUM INDUM L. (Hohnel, 1, p. 36)		Java?	×												0.33	
DIPHYSA CARTHAGENÉNSIS Jacq.		Panama		×	×	×	×	×					×		0.16	155–160
ENTEROLOBIUM SCHOMBERGKII Benth.		"	×							×	×			×		
" sp ?	Piñon	Colombia	×						×		×			×	0.33	75
ERYTHRINA CRISTA-GALLI L.		Brazil		×		×		×			×			×	0.18	135–140
" FALCATA Benth.	Ceibo	Argentina		×		×		×		×	×			×		
" INDICA Lam.	Dap-dap	Philippine Islands		×		×		×			×				0.26–0.28	90– 95
" MONOSPERMA Gaudich.	Wili-wili	Hawaii		×		×		×					×		0.19–0.20	125–130
" aff. VELUTINA Willd.		Curaçao		×		×		×				×			0.19	130

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Scientific name	Common name	Country	Elements storied				Regularity of lines				Visibility				Measurements	
			All elements	Rays not storied	Wood parenchyma cells storied	Fiber pits storied	Regular	Fairly regular	Irregular	Local occurrence	Distinct—fairly so	Barely visible	Lens required	Indistinct with lens	Tier-height in Mm.	Number of tiers per inch
LEGUMINOSAE—*Continued*																
GENISTA CANARIENSIS L. (Hohnel, 1, p. 38)			×													
GOURLIEA DECORTICANS Gill. (four specimens)	Chañar	Argentina	×				×						×		0.13–0.15	165–185
HERMINIERA ELAPHROXYLON Guill. & Perr. (Jaensch, 3, p. 268)	Ambatsch	India		×		×		×					×		0.22–0.23	
HOLOCALYX BALANSAE Micheli	Alécrin	Argentina	×				×					×			0.20–0.21	120–125
ICTHYOMETHIA PISCIPULA (L.) Kuntze	Jamaica Dogwood	Florida	×		×		×	—					×		0.17–0.18	140–150
INDIGOFERA ZOLLINGERIANA Miq.		Philippine Islands	×						×			×	—		0 18	135
INOCARPUS EDULIS Forst. (Hohnel, 1, p. 33)	Boko or Coco Wood	Guiana	×			×	×				×				0.33	
KOOMPASSIA EXCELSA Teub.	Manggis	Philippine Islands	×					×			×				0.55–0.60	42–45
LABURNUM VULGARE J. Presl (Wiesner, 5, p. 940)	Goldregen	Europe		×												
LONCHOCARPUS ALBIFLORUS G. Don	Robo blanco	Argentina	×		×		×					×			0.21	118–121
MACHAERIUM WHITFORDII Macb.	Negrillo	Colombia	×			×	×						×		0.17–0.18	140–145
" sp ? (*Dalbergia*?)	Jacaranda roxo	Brazil	×					×					×		0.19	128
" sp.? (*Dalbergia*?)	Jacaranda mulatto	"	×					×				×			0.19	128
" sp.? (*Dalbergia*?)	Jacaranda	"	×					×					×		0.18	136
MEZONEURUM KAUAIENSE Hillebd.	Uhi-uhi	Hawaii		×					×			×			0.23–0 25	100–110
MILLETIA PENDULA Benth.		India	×				×				×				0.24–0 25	98–104

MYROCARPUS FASTIGIATUS Allem	Incienso	Argentina	×			×				×				0 26	95
" "	Oleo vermelho	Brazil	×			×				×				0 28	90
" FRONDOSUS Allem	Incienso	Argentina	×			×				×				0 21–0 23	110–118
" "	"	"	×			×				×				0 19	128
" " ?	Cabriuva	Brazil	×			×					×			0 18–0 19	132–136
MYROSPERMUM FRUTESCENS Jacq	Cereipo	Venezuela	×			×				×				0 25	100–102
" sp	"	"	×			×				×				0 26–0 28	90– 95
MYROXYLON TOLUIFERUM H B K (*Toluifera balsamum* L)	Balsamo de Tolu	Colombia	×			×				×				0 23	109
MYROXYLON TOLUIFERUM ?	Balsamo cope	"	×			×				×				0 25	102
OLNEYA TESOTA Gray	Ironwood	Southwestern United States		×			×						×	0 16–0 17	150–160
ORMOSIA CALAVENSIS Azaola		Philippine Islands	×					×	×	×				0 36	70
" ROBUSTA Baker		India	×					×		×				0 37	68– 70
OUGEINIA DALBERGIOIDES Benth	Sandan		×				×				×			0 16	154–160
" "	"	"	×			×					×			0 20	125
PARKIA BIGLANDULOSA Wight & Arn (Hohnel, I, p 38)		Malava?	×			×								0 20	
PLATYMISCIUM DUBIUM Pittier		Panama	×					×		×				0 23–0 25	102–108
" sp (No 428)	Trebo	Colombia	×				×			×				0 27–0 28	88– 94
" sp (No 404)	"	"	×			×				×				0 25	98–100
PLATYPODIUM MAXONIANUM Pittier		Panama	×			×				×				0 22–0 24	105–115
PONGAMIA GLABRA Vent (Solereder 6 p 903)		Tropical Asia													
PONGAMIA MITIS Merr		Philippine Islands	×			×					×			0 16	155–160
PTEROCARPUS ANGOLENSIS DC (Hohnel I, p 34)	Barwood		×			×								0 25?	
PTEROCARPUS DALBERGIOIDES Roxb	Andaman Padouk	India	×			×					×			0 22–0 23	112–117
" DRACO L	Pao sangue	Brazil	×				×				×			0 20–0 21	120–125
" ECHINATUS Pers	Prickly Narra	Philippine Islands	×				×				×			0 21	120
" ERINACEUS Lam (Hohnel I p 34)		Senegal	×			×					×			0 20?	
PTEROCARPUS INDICUS Willd	Red Narra	Philippine Islands	×			×								0 20–0 21	120–125
" MACROCARPUS Kurz	Padouk	India	×			×					×			0 23–0 24	106–110
" MARSUPIUM Roxb	Vengai		×			×				×				0 21–0 22	115–120
" "	Bija Sal	"	×			×					×			0 23	110

TABLE OF WOODS WITH TIER-LIKE STRUCTURE, SHOWING THE ELEMENTS STORIED, THE REGULARITY AND VISIBILITY OF THE TRANSVERSE LINES ("RIPPLE MARKS"), AND MEASUREMENTS OF TIER-HEIGHT—*Continued*

Scientific name	Common name	Country	Elements storied: All elements	Elements storied: Rays not storied	Elements storied: Wood parenchyma cells storied	Elements storied: Fiber pits storied	Regularity of lines: Regular	Regularity of lines: Fairly regular	Regularity of lines: Irregular	Regularity of lines: Local occurrence	Visibility: Distinct—fairly so	Visibility: Barely visible	Visibility: Lens required	Visibility: Indistinct with lens	Measurements: Tier height in mm	Measurements: Number of tiers per inch
LEGUMINOSAE—*Continued*																
PTEROCARPUS ROHRII Vahl?		Brazil	×					×				×			0 26	95
" SANTALINUS L	Red Sanders	India	×				×					×			0 22	113
PTEROGYNE NITENS Tul (four specimens)	Ibiraro or Viraro	Argentina	×				×					×			0 25–0 28	90–100
" sp ?	Cereipo	Venezuela	×				×					×			0 26	94
SOPHORA CHRYSOPHYLLA Seem	Mamani	Hawaii		×				×					×		0 16	155–160
" SECUNDIFLORA Lag	Frijolita	Southwestern United States		×				×					×	×	0 16	160
SWARTZIA GAILLARDI Pittier		Panama	×					×				×			0 22–0 23	110–115
" PANAMENSIS Benth		"	×				×				×				0 25	100–102
" TOMENTOSA DC (Stone and Freeman, 9, p 55)	Wamara	British Guiana	×					?				×				
TAMARINDUS INDICA L.	Tamarind	Hawaii	×						×			×			0 31	80
TIPUANA SPECIOSA Benth	Tipa	Argentina	×				×				×				0 20–0 21	120–125
" sp (No. 897)	"	"	×				×				×				0 18–0 19	130–135
WALLACEODENDRON CELEBICUM Koord	Banuyo	Philippine Islands	×						×		×				0 33–0 36	70–75
LYTHRACEAE (see page 260)																
PHYSOCALYMMA SCABERRIMUM Pohl?	Brazilian Tulip	Brazil	×			×	×						×		0 16	160
MALVACEAE																
GOSSYPIUM ARBOREUM L.	Cotton	Costa Rica		×					×			×			0 29	85

GOSSYPIUM DRYNARIOIDES Seem.	Kokio	Hawaii		×	×				×					×		
HIBISCUS GREWIAEFOLIUS Hassk.		Philippine Islands	×				×				×				0.33–0.36	70– 75
" MACROPHYLLUS Roxb.		Java		×					×							
" SIMILIS Blume (M.&J., 7, I, p 375)		"		×					×							
HIBISCUS TILIACEUS L.	Malubago	Philippine Islands	×	—			×	—			×				0 28–0.30	85– 90
SIDA DENSIFLORA Hook. & Arn.	Loro blanco			×				×			×				0.23	110
THESPESIA POPULNEA Corr. (M.&J., 7, I, p. 389)		India	×	—				×			×			×	0.25	100
MELIACEAE																
CARAPA GUIANENSIS Aubl.?	Andiroba	South America	×						×		×			×	0.50	50
" OBOVATA Blume (M &J, 7, II, p. 200)		Java	×					×				×				
CEDRELA sp. (four specimens)	Cedro	Tropical America	×						×	×	×			×	0 45–0.50	50– 55
CHICKRASSIA TABULARIS A. Juss (*Chukrasia tabularis* A Juss)	Chittagong Wood	India	×						×	×	×				0 31–0 32	78– 82
ENTANDROPHRAGMA CANDOLLEI Harms	Sapeli	Africa	×						×	×	×			×	0 5	50
GUAREA TRICHILOIDES L. (Hohnel, 1, p. 39)			×				×									
KHAYA sp.	African Mahogany	Africa	×						×	×	×			×	0 50	50
SWIETENIA MAHAGONI Jacq.	Mahogany, Caoba	Tropical America	×					×	—	—	×				0 46–0 54	46– 54
MORACEAE																
FICUS ALTISSIMA Blume		India	×					×			×			×	0 38–0 40	62– 66
" BENJAMINA L.	Balete	Philippine Islands	×					×			×			×	0.39	64
MORINGACEAE																
MORINGIA PTERYGOSPERMA Gartn (Hohnel, 1, p. 35)	Griesholz		×	—					×	×	×					
MORINGIA sp. (M &J, 7, II, p 514)		Java	×					×			×					
ROSACEAE (see page 260)																
FEROLIA GUYANENSIS Aubl ? (*Parinarium* sp, Hohnel, 1, p. 43)	Ficatin- or Konigsholz	Guiana	×				×									

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RUTACEAE																
CHLOROXYLON SWIETENIA DC.	Satinwood	India	×					×			×				0 31–0 32	78– 82
SAPINDACEAE																
SAPINDUS SENEGALENSIS Poir. (Hohnel, 1, 43)		Africa?		×		×	×						×		0 20	
SIMARUBACEAE																
PICKRAENA EXCELSA Lindl. (Hohnel, 1, p. 41; Wiesner, 5, p. 955)	Jamaica Quassia	West Indies	—	×			?						×			
PICRASMA JAVANICA Blume (M &J., 7, II, 84)		Java	×				×				×				0 30	
SIMARUBA AMARA Aubl.	Pao parahyba	Brazil	×					×			×				0 43	58– 60
" GLAUCA DC.	Bitterwood	Florida	×					×	—		×				0 50	51– 52
SURIANA MARITIMA L.?	Palo corra	Curaçao	×					×				×			0 21	120
STERCULIACEAE																
GUAZUMA ULMIFOLIA Lam.	Guasima	Curaçao		×					×			×			0 30–0.31	80– 85
HERITIERA LITTORALIS Ait.	Dungon late	Philippine Islands		×				—	×			×			0 31	80
" MINOR Lam.	Sundri	India		×				—	×			×			0 31–0 32	77– 80
" "	"	"		×				×				×			0.27	92
KLEINHOVIA HOSPITA L.		"	×	—				×				×			0.31–0.33	74– 80

MELOCHIA INDICA Gray (M.&J., 7, I, p. 469)		Java	X	—				X			X					
PTEROCYMBIUM JAVANICUM R.Br. (M.& J., 7, I, p. 440)		"		X				X				X			0.40	
PTEROCYMBIUM TINCTORIUM Merr.		Philippine Islands		X	X	X		X			X				0.45–0.50	50– 55
PTEROSPERMUM DIVERSIFOLIUM Blume		Java		X			X	—			X	—			0.50	
" JAVANICUM Jungh. (M.& J., 7, I, p. 463)		"		X			X	—			X	—			0.50	
PTEROSPERMUM SUBERIFOLIUM Lam. (Höhnel, I, p. 42)		India	X	—				X			X			X	0.30–0.31 (0.25,H.)	80– 85
PTEROSPERMUM sp.	Bayok	Philippine Islands	X					X			X				0.38	66
STERCULIA FOETIDA L. (M.&J., 7, p. 424)		Java		X	X											
" POPULIFOLIA Roxb.	Dalibuda	India		X	X			X			X				0.36	70
TARRIETIA ARGYRODENDRON Benth.	Crow's-foot Elm	Australia		X				X			X				0.36	70
" JAVANICA Blume	Lumbayao	Philippine Islands		X				X			X				0.36–0.41	60– 70
" SUMATRANA Miq. (M.&J., 7, I, p. 446)		Java		X				X			X				0.30	
TARRIETIA SYLVATICA (Vidal) Merr.	Dungon	Philippine Islands		X				X			X				0.32–0.33	83– 85
" "	"	" "		X				X				X			0.26–0.28	90– 95
TILIACEAE																
BERRIA AMMONILLA Roxb.		Java	X	—				X			X				0.25	
" QUINQUELOCULARIS T.&B. (M.& J., 7, I, pp. 492, 496)		"		X					X	X						
COLUMBIA SERRATIFOLIA DC.	Analin	Philippine Islands	—	X				X			X				0.31–0.33	75– 80
DIPLODISCUS PANICULATUS Turcz.	Baloba	" "	X					X			X				0.31–0.33	75– 80
GREWIA CELTIDIFOLIA Juss.		Java		X				X			X					
" LAEVIGATA Vahl (M.&J., 7, I, pp. 499, 507)		"		X				X			X				0.23	
GREWIA ROLFEI Merr.	Danglin	Philippine Islands		X				X				X			0.24–0.25	100–105
" TILIAEFOLIA Vahl		India		X				X				X			0.23	110
HELIOCARPUS AMERICANUS L.	Amor seco	Argentina		X				X				X			0.33	75
" APPENDICULATUS Turcz.		Panama		X	X				X		X				0.38	65
PENTACE POLYANTHA Hassk. (M.&J., 7, p. 488)		Java	X					X			X				0.40	
SCHOUTENIA OVATA Korth. (M.&J., 7, I, p. 522)		"	—	X				X	—		X	—			0.22	

TABLE OF WOODS WITH TIER-LIKE STRUCTURE, SHOWING THE ELEMENTS STORIED, THE REGULARITY AND VISIBILITY OF THE TRANSVERSE LINES ("RIPPLE MARKS"), AND MEASUREMENTS OF TIER-HEIGHT—*Continued*

Scientific name	Common name	Country	Elements storied: All elements	Elements storied: Rays not storied	Elements storied: Wood parenchyma cells storied	Elements storied: Fiber pits storied	Regularity of lines: Regular	Regularity of lines: Fairly regular	Regularity of lines: Irregular	Regularity of lines: Local occurrence	Visibility: Distinct—fairly so	Visibility: Barely visible	Visibility: Lens required	Visibility: Indistinct with lens	Measurements: Tier height in mm	Measurements: Number of tiers per inch
TILIACEAE—*Continued*																
TILIA AMERICANA L	Basswood	Eastern United States		×				×	—			×		×	0 42–0 45	55– 60
" CORDATA Mill. var JAPONICA		Japan		×				×				×		×	0 48	52
" HETEROPHYLLA Vent	Basswood	Southeastern United States		×				×	—			×		×	0 40–0 41	60– 62
" MANDSHURICA Rupr		China		×				×				×		×	0 45	56
" PUBESCENS Ait (Record, 8, p 76)	Basswood	Eastern United States		×				×	—			×		×	0 41–0 43	58– 60
ULMACEAE																
HOLOPTELEA INTEGRIFOLIA (Roxb.) Planch (*Ulmus integrifolia* Roxb)		India	×					×					×		0 22–0 23	110–115
ZYGOPHYLLACEAE																
BULNESIA ARBOREA (Jacq) Engl	Vera	Venezuela	×				×						×		0 10	250 ±
" SARMIENTI Lorentz	Palo santo	Argentina	×				×						×		0 10	240–250
GUAIACUM COULTERI Gray	Guayacan	West Coast Mexico	×				×						×		0 09	260–270
" OFFICINALE L	Lignumvitae	West Indies	×				×						×		0 10	250–260
" SANCTUM L	"	Florida	×				×						×		0 09	260–270
LARREA CUNEIFOLIA Cav (Solereder, 6, p 182)		Argentina?														
LARREA DIVARICATA Cav	Javilla	"	×				×	—					×		0 09	270–280
PORLIERA HYGROMETRA Ruiz & Pav (*Guaiacum hygrometricum* Bail, Hohnel, 1, p 40)	Guayac	Chile	×				×						×		0 09–0 10	

SUMMARY

Storied or tier-like arrangement of part or all of the elements is characteristic of many dicotyledonous woods representing a wide range of natural orders and families. The storied structure is found also in the secondary phloëm.

The structure is exhibited on longitudinal sections, typically the tangential, as fine transverse striations ("ripple marks"). These are often visible without a lens.

"Ripple marks" are constant enough in stems of considerable thickness to serve as a valuable diagnostic feature.

In some woods pit areas on the fibers are in seriation. In some instances, also, the cells of the wood parenchyma strands are arranged in a secondary seriation, visible under the lens.

A table is appended giving for each wood the various elements storied, the uniformity and distinctness of the markings, and the height of the tiers.

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The ancestry of maize—a reply to criticism

Paul Weatherwax

In a recent article by H. J. Kempton (1), of the Bureau of Plant Industry, exception is taken to some statements made by me in a paper appearing last September in the Bulletin of the Torrey Botanical Club (45: 309–342), on the evolution of maize. Inasmuch as some real errors are pointed out in this criticism, their correction is in order; but, as to certain other points upon which our data differ, I have nothing to add to my original paper. Our differences of opinion on matters of interpretation and evaluation of facts would probably not be diminished by further discussion; and any criticism on ethical grounds of the spirit of Kempton's paper and his imputations of the writer's ignorance are left to the fair judgment of the reader. But Kempton's manner of treating details and his intermingling of the irrelevant with the relevant have clouded the issue, and a brief presentation of its present status seems appropriate.

It is said (p. 4) that I have misrepresented Collins (2) by confusing bracts with prophylla and by substituting "one-rowed" for "single-rowed" in a quotation. Both points are well taken, for no misrepresentation was intended. These errors had been discovered long before the appearance of Kempton's paper, and steps had already been taken to correct them; this is a welcome opportunity to do so.

The error in speaking of the husk of the maize ear as prophylla (pp. 314, 330) does involve an unintentional misrepresentation of Collins's statement; but this point is beside the question, for the true prophylla of all kinds of maize, including pod corn, have buds in their axils, which is the significant point. Whether or not these buds develop far enough to be visible externally is a quantitative matter. The difference between "one" and "single" in the quotation (p. 321), describing the pistillate spike of teosinte, is appreciated, and it is unfortunate that the substitution was made. But the bearing of this point upon the evolution of

the ear is unchanged, for the fact remains that Collins (p. 525, footnote) was using the structure of the spike of teosinte in an attempt to explain the appearance of ears with odd numbers of rows in some hybrids between maize and teosinte; and a "single-rowed" spike, such as that of teosinte, is of no avail in getting around the difficulty, for it has *two* rows of functional spikelets, not to mention the aborted ones.

Kempton's support (pp. 6–7) of the theory that the ear of maize originated by fasciation is based chiefly upon certain true-breeding races having bifurcated ears and a bifurcated central spike in the tassel. But our only evidence of the regressive nature of these mutants is the fasciation theory itself, and reasoning of this kind does not make much progress. The fact that ears having rows not in multiples of four could not have been formed by the union of spikes having four rows each is evaded by Kempton's assumption (p. 7) that a row of pairs of spikelets or the pedicelled spikelets of two such rows were aborted. Abortion of parts is a common occurrence in maize, but our best evidence of this is in finding their rudiments; and, if abortion is thought to be responsible for the occurrence of ears with ten, fourteen, or eighteen rows, the burden of proof is with those who reject a more simple and more direct explanation of the situation. Such an explanation is afforded by the theory that the ear and the central spike of the tassel have developed from a branched inflorescence like that of some of the sorghums. The assumption here involved is that the pairs of spikelets are the remnants of reduced branches; and material illustrative of intermediate steps in this reduction is afforded by branch corn, which was unknown when Collins (p. 526) rejected this theory.

Advocates of the hypothesis that maize arose by hybridization find the necessity for their position in the fact that ordinary maize has so many primitive characteristics and seems to occupy an intermediate position between teosinte, which is more highly specialized, and pod corn, which seems to be more primitive than ordinary maize.

A detailed morphological study shows that the differences in specialization here concerned are neither so great nor so significant as was supposed when the hypothesis was first advanced; but further discussion of this point is waived for the present.

The primitive characters of the maize plant might cause some difficulty in connection with any theory to the effect that maize descended from teosinte itself or from some plant much like teosinte; but probably no one at present gives serious consideration to any such theory. In descending directly from a primitive ancestor, the plant need not have made equal progress in all respects, and a combination of highly specialized characters with others relatively simple would be expected. Probably no one appreciates more fully than does the systematist the significance of this principle.

The weakest spot in the hypothesis of the hybrid origin of *Zea* lies in the fact that pod corn has not been shown to be essentially different from ordinary corn except in the possession of enlarged bracts and of functional pistils in the tassel. In Collins's argument, pod corn has no exact identity. Sometimes it has ears, and sometimes it is earless. He seems to have selected from all the characteristics possessed by this ill-defined variety those tending to uphold his hypothesis. Kempton admits as much (p. 7) when he attributes the presence of buds in the axils of the leaves of pod corn to the recent origin of this variety from ordinary corn. The problem for which they offer no solution involves a means of distinguishing the characters of the orthodox podded type—one of the hypothetical ancestors of *Zea*, according to their view—from other characters received from ordinary maize by this recent mutant. It is true that the hybrid-origin hypothesis itself will distinguish them, but, when we apply it, we find ourselves dealing in circular logic. It is generally admitted that the podded types now in existence are recent mutations rather than original forms; but our criterion for the regressive nature of some of their characteristics is in the character of the grasses held to be closely related to maize.

The idea of the hybrid origin of maize has had the misfortune to be based upon a hypothesis not substantiated by subsequently discovered facts. It has never been very enthusaistically accepted by botanists in general, because it seems unreasonable and taxes the imagination unnecessarily. It has had its good effect in promoting further investigation, but it has run its course and has been found wanting.

On the other hand, comparative morphology, which has been one of the most reliable and productive agents in establishing lasting theories of evolution, points out clear-cut, logical, reasonable evidence of the direct origin of *Zea*, coördinately with *Euchlaena* and *Tripsacum*, from an ancestor long ago extinct. There has been pointed out no accepted fact whose rational interpretation discloses any inconsistency in the theory. The three genera are different simply because they have lost different organs that were possessed by their progenitor and have specialized others to different degrees.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1911–1919

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Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

This Index is reprinted monthly on cards, and furnished in this form to subscribers at the rate of one cent for each card. Selections of cards are not permitted; each subscriber must take all cards published during the term of his subscription. Correspondence relating to the card issue should be addressed to the Treasurer of the Torrey Botanical Club.

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BULLETIN

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AUGUST, 1919

A new Matonidium from Colorado, with remarks on the distribution of the Matoniaceae

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(WITH PLATES 12 AND 13 AND TWO TEXT FIGURES)

In 1916 Professor Cockerell, of the University of Colorado, published a brief note* based upon plant material collected from the supposed McElmo formation of southwestern Colorado. The subsequent discovery that this supposed Lower Cretaceous flora was stratigraphically above a black shale horizon carrying a considerable dicotyledonous flora led to the sending of all of the material to the present writer for a more critical study than Professor Cockerell was able to devote to it.

The discussion of the question of the stratigraphic relations and age of these two floras is reserved for a subsequent communication, the present paper being devoted to the interesting questions of habit and distribution derived from a study of the abundant relics of *Matonidium* preserved in the later of the two floras above mentioned.

The Colorado remains, which Professor Cockerell identified as *Matonidium Althausii*, or *Matonidium Goepperti* as some paleobotanists prefer to call the species on the ground that the older and correct name is less familiar, are superficially very much like that well-known and rather variable species. Botanists who

* A Lower Cretaceous flora in Colorado. Jour. Wash. Acad. Sci. 6. 109–112. *pl. 1, 2.* 1916.

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depreciate specific differentiation and who, like Professor Seward, are more interested in the former distribution of generic types, would not hesitate to refer the Colorado form to *Matonidium Althausii.* Such questions are always difficult, and tastes and temperaments differ with individual workers. One point of view may serve one purpose and the other another. All that need be insisted upon in the present connection is that the framing of loosely defined specific limits as opposed to finely discriminated ones effectually obscures whatever value the fossils may have for the elucidation of geologic chronology or problems of the former time and avenues of migration, and is a method that has gradually become almost obsolete in the allied field of paleozoölogy.

It would seem *a priori* incredible that a single botanical species should range through the Jurassic and Lower Cretaceous and extend over at least two continents in opposite hemispheres; nevertheless it is impossible to differentiate the British Jurassic from the Wealden forms or these from the still younger Russian occurrences, and the specimens referred by Ward to *Matonidium Althausii* from the Albian Fuson formation of the Black Hills* in this country cannot be distinguished from the earlier European occurrences of that species.

Recognizing fully the individual variability in *Matonidium Althausii* and the variation in the form and size of the pinnules from different parts of a single frond, the Colorado *Matonidium* nevertheless presents a number of apparently constant peculiarities that serve to mark it as a slightly but consistently different type. Among these distinctive features might be mentioned the stouter stipe and rachises, the more numerous pinnae, which appear to have been at least twice as numerous as in *Matonidium Althausii*, judging from the frond bases of the latter as figured by Ettingshausen, Schenk and Seward. The pinnae are more slender in the Colorado form and the pinnules are shorter and wider with fewer and more nearly circular or isodiametric sori. For example, in the form of *Matinidium Althausii* described from the Black Hills the falcate slender pinnules are twice as long as in the Colorado material, and each bears about twelve pairs of sori. The Portuguese specimens as figured by Heer† show eighteen pairs of

* Ann. Rep. U. S. Geol. Surv. 19^2: 653. *pl. 160, f. 5–8.* 1899.

† Secc. Trab. Geol. Port. 16. *pl. 15, f. 1–6.* 1881.

sori to each pinnule, Schenk's admirable figures* show eight or nine pairs, and they are very numerous in Trautschold's figures of the Russian material.† The most elongate and largest pinnules of the Colorado species bear but five or six sori on the distal half of the lamina and but six or seven on the proximal half, while the most abundant remains are those with short and broad pinnules bearing three sori on their distal halves and four sori on their proximal halves.

I regard these features and others to be mentioned as of specific value and propose that the Colorado specimens be discriminated as

Matonidium americanum, sp. nov.

Matonidium Althausii Cockerell, Jour. Wash. Acad. Sci. **6**: 111. *f. 2.* 1916. [Not (Dunker) Ward.]

Cycadospadix? sp. Cockerell, *Idem.* 110. *f. 1.*

This species also includes forms which Cockerell suggested might represent *Todites*, and *Weichselia* or *Cladophlebis*. The equisetaceous stems mentioned as probably representing *Equisetum Burchardti* (Dunker) Brongniart are probably fragments of the large stipes of *Matonidium*. The striations are somewhat irregular and do not alternate at the nodes, there are no traces of nodal sheaths and the apparent jointing appears to be due to shrinkage cracks of a collapsed and consequently furrowed stipe, since a similar state of preservation is seen in the objects that were referred to *Cycadospadix*, which latter are clearly the apical portions of *Matonidium* stipes and only most superficially suggestive of *Cycadospadix*, and strictly comparable with similar remains of *Matonidium Althausii* as figured by Schenk,‡ Ettingshausen § and Seward.||

Matonidium americanum may be characterized as follows: Digitate fronds with the same habit as *Matonidium Althausii* or the existing *Matonia pectinata*, with long stout stipes about 1 cm. in diameter as preserved in a partially flattened condition. Stipe surface somewhat regularly furrowed, but whether this was

* Palaeont. **19** 220. *pl. 27, f. 5; pl. 28, f. 1, 2, pl. 30, f 3, pl. 42, f 1.* 1871

† Nouv. Mém. Sci. Nat. Moscou **13** 28. *pl. 19, f 3* 1870

‡ Palaeont. **19**: *pl. 42 f. 1.* 1871.

§ Abh. k. k. Geol. Reichs. **13**: *pl. 5, f. 4, 6.* 1854.

|| Jurassic Fl. **1**: *pl. 11, f. 1.* 1900.

an original feature or is due to collapse during fossilization is undeterminable. Distad the stipe expands into a flabellate recurved or reflexed "collar" which shortly divides to form the axes of the pinnae, whose attitude in life was transverse or reflexed with respect to that of the vertical stipe. These reflexed "collars" are especially common in the rocks and are the objects which Cockerell referred to *Cycadospadix*. They are well shown in PLATE 12, FIGS. 9–12.

The width of the "collar" before it split up into pinnae varies from specimen to specimen and is not always clear, although it is narrowest medianly. No traces of pinnules have been found in actual connection with these stipes although they are in close association. The divisions of the "collars," however, do not terminate as they would if the fossils were of the nature of *Cycadospadix*, and the breaks at the ends are obviously mechanical and not natural. The evidence of their reflexed form is also clear, and the size of the segments, their condition of preservation and furrowing are in exact agreement with the specimens of proximal pinnae axes. The number of pinnae was large but somewhat variable. The "collar" shown in FIG. 9. indicates four lateral pinnae at each end of the collar and thirty-one additional intercalated pinnae, making thirty-nine in all. FIG. 10 shows clear traces of at least twenty-five pinnae, and FIG. 12, which is the counterpart of the apex of the specimen shown in FIG. 11, shows the bases of thirty-six pinnae. The pinnae were therefore much more numerous than the published figures indicate for *Matonidium Althausii* and also somewhat more numerous than the normal number in the modern *Matonia pectinata*. The exact length of the pinnae is unknown since all are preserved in a fragmentary condition, but judging by the fragments of proximal, medial and distal parts preserved, and the size and degree of tapering of the rachises, they could not well have been shorter than 20–25 cm., or about the same length as in the admirable specimen of *Matonidium Althausii* figured by Schenk* from the German Wealden. Their width, however, was much less than in that species, the largest certainly identified (PLATE 12, FIG. 8) being but 11 mm. across, while the more abund-

* Palaeont. 19: *pl. 28, f. 1.* 1871.

ant remains (PLATE 12, FIG. 2) are about 8 mm. in width. Several sterile fragments which I have referred to this species on the basis of general form and association are somewhat larger (PLATE 12, FIG. 7) being 15 mm. wide. These show a narrower rachis with slightly less obtuse pinnules which are greatly crowded, and may represent fragments of a contemporaneous species of *Cladophlebis*. Fertile fragments of pinnae present a very different appearance when the opposite faces are viewed. From below the rachis appears very stout and the laminae of the pinnules is entirely hidden by the large sori except for a broad band in the position of the midvein. Viewed from above the rachis is much narrower, the pinnules evidently having been inserted near the upper margin of the rachis as shown in the section (PLATE 13, FIG. 4).

The pinnules are short and broad, more or less falcate, obtusely rounded at their tips. All have revolute margins and they are opposite or sub-opposite in position. Their substance is thick and the venation cannot be made out in any of the preserved material. Distad along the rachis the pinnules gradually become shorter and somewhat broader relatively (PLATE 12, FIG. 6), eventually becoming very small and coalescent basally (PLATE 12, FIG. 3, 4), their revolute margins giving them a pointed appearance. Proximad along the rachis the pinnules gradate through short and broad forms to short wide scallops as shown in PLATE 12, FIG. 5.

The sori are in two rows separated by a broad space in the region of the midrib. They diminish in size toward the pinnule tips and are prevailingly circular except where mutual crowding causes the lateral margins to be somewhat flattened. They stand out from the surface of the pinnules as prominent umbos and a pronounced umbilicus on the indusium marks the position of the central soral axis. The indusia are peltate and are intact in all of the Colorado material so that the number of sporangia can not be made out. In *Matonidium Althausii* the sori are said to have been more numerous than in the modern *Matonia pectinata*, sections of a sorus of the latter species being introduced for comparison on PLATE 13, FIGS. 1, 2. In the bulk of the material each pinnule shows three or four upper and four or five lower sori (PLATE 13, FIG. 3). These were the only forms in the collection which Professor Cockerell had labelled *Matonidium Althausii*. In the

largest fruiting material there are six or seven sori on the distal halves of the pinnules and seven or eight on their proximal halves, (PLATE 13, FIG. 6), a less number than in *Matonidium Althausii*, as already remarked. The sori also differ from those of the latter in being isodiametric instead of transversely elongate and more or less rectangular.

The material, which was collected by J. T. Duce, comes from the divide between Cutthroat Gulch and Hovenweep Canyon west of Dolores and is contained in a light somewhat ferruginous sandstone containing little quartz and a great deal of feldspar, and apparently corresponds to what Cross correlated with the Dakota sandstone in the San Juan region of Colorado.

The family Matoniaceae is one of exceptional botanical interest. Its sole existing genus, *Matonia* R. Brown (1830), contains but two known species which differ remarkably in vegetative habit and are both confined to the uplands of the Malay Peninsula and the island of Borneo. The older and only species known up to 1888 was commonly associated with the family Cyatheaceae, although its intermediate character had usually resulted in its being set apart as a special tribe. It has also been associated with the Gleicheniaceae and the Polypodiaceae. Christ (1897) and most subsequent workers have regarded *Matonia* as the sole existing type of a distinct family, and an admirable account of the genus and of some of its fossil relatives was given by Seward in 1899.*

The extinct genus *Matonidium*, to which the Colorado plant is referred, was a characteristic type of the Jurassic and especially of the Lower Cretaceous. Although known as early as 1843 its botanical affinity was first recognized by Schenk in 1871 and it has subsequently been found to have been widespread in the European region and more sparingly represented in the western United States. Most of the occurrences have been referred to the single species *Matonidium Althausii*, although Krasser† has described a well characterized species from the Upper Cretaceous (Cenomanian) rocks of Moravia, which appears to have also been present in rocks of the same age in Bohemia.

* Phil. Trans. Roy. Soc. Lond. 191B: 171–209. *pl. 17–20.* 1899.

† Beitr. Paläon. Oesterreich-Ungarns 10: 119. *pl. 11, f. 1; pl. 12, f. 1, 2; pl. 17, f. 10.* 1896.

These occurrences are assembled upon the accompanying sketch map (TEXT FIG. 1) and are shown within the enclosed areas in Europe and North America. The area of distribution of the two existing species of *Matonia* is shown on the map in solid black. A second rather well-known extinct genus belonging to this family is the genus *Laccopteris*, which was founded by Presl in 1838. *Laccopteris* was especially characteristic of the late Triassic and hence was considerably older in its inception than *Matonidium*. Its relationship with *Matonia* was first clearly defined by Zeiller*

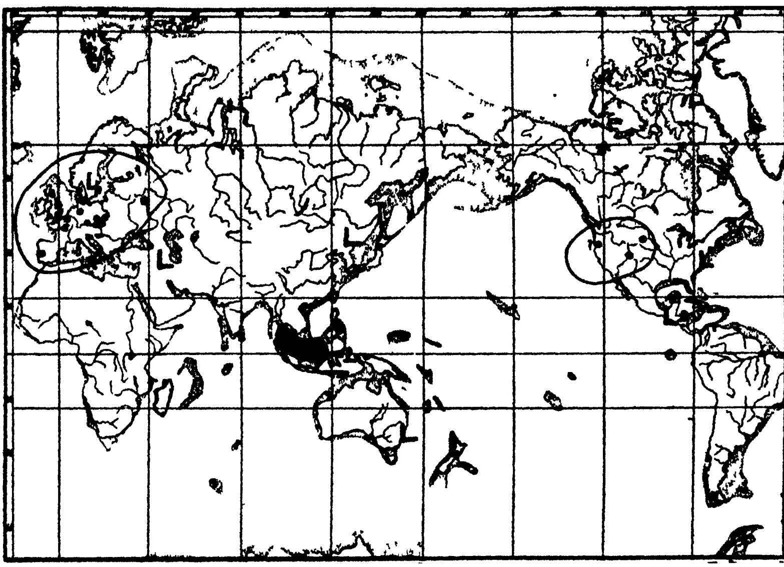

FIG. 1. Sketch map showing the area of distribution of the two existing species of *Matonia* (solid black), the fossil occurrences of *Matonidium* (black disks within the enclosed areas), and the fossil occurrences of *Laccopteris* where they do not coincide with occurrences of *Matonidium* (L).

in 1885. Reference to the accompanying map (TEXT FIG. 1), where the occurrences of *Laccopteris* are indicated by L, shows that it greatly extends the Mesozoic range of the family and gives the Matoniaceae representation in the far north (Greenland and Spitzbergen), in the Asiatic region and in Australia. Other and less well known fossil genera which have been referred to the Matoniaceae include *Phlebopteris* Brongniart, *Microdictyon* Saporta and *Knowltonella* Berry.

* Bull. Soc. Bot. France 32: 22. 1885.

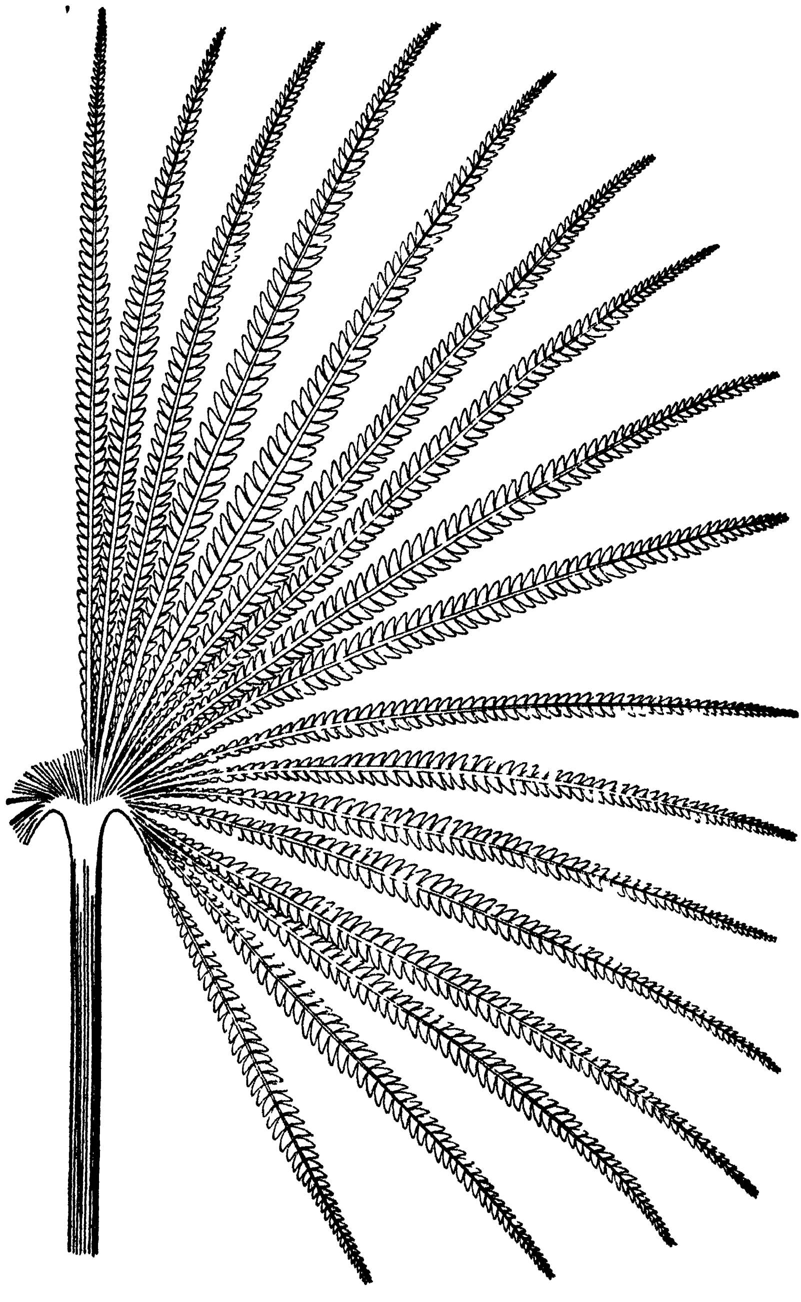

FIG 2 Restoration of *Matonidium americanum* Berry, two fifths natural

The accompanying restoration of *Matonidium americanum*, shown in TEXT FIG. 2, is based upon a considerable amount of material which, although fragmentary, supplies data for all parts of the frond. Its abundance in the small collection from this one locality would seem to indicate that the species was gregarious, sending up its stout stipes from a creeping rhizome as does the modern *Matonia pectinata*. The reduced figure was made from a life size drawing made by plotting the various fragments of the different parts to scale, and the arrangement of the pinnae is based upon their disposition in *Matonia pectinata* and the evidence derived from the numerous fossil frond bases ("collars") preserved. Whether the stipe in the fossil species was as elongated as in the modern *Matonia pectinata* is not known. At the apex the stipe of *Matonidium americanum* was less distinctly dichotomous with less scirpoid branches than in *Matonia pectinata*, one side of the stipe becoming concave and the whole forming a reflexed fan-like base from which the rachises of the numerous pinnae proceeded. In life these were not upright as in the restoration but were turned back ninety degrees or more giving the fronds an almost peltate appearance.

Explanation of plates 12 and 13

PLATE 12

MATONIDIUM AMERICANUM Berry

FIG. 1. Under side of fertile pinna showing stout furrowed rachis.
FIG. 2. Under side of fertile pinna showing normal size and form.
FIG. 3. Upper side of apical portion of pinna.
FIG. 4. Portion of same, × 10.
FIG. 5. Basal part of pinna from below.
FIG. 6. Upper part of pinna from above.
FIG. 7. Maximum size of rare occurrence, from above.
FIG. 8. Fragment from below showing maximum development of sori.
FIG. 9. Apex of stipe showing indications of 39 pinnae.
FIG. 10. Apex of stipe with 25 pinnae.
FIG. 11. Apex of stipe of another specimen.
FIG. 12. Counterpart of apex of specimen shown in 11 with indications of 36 pinnae.

PLATE 13

FIGS. 1, 2. MATONIA PECTINATA R. Br.

FIG. 1. Lamina and sorus in vertical section showing indusium (black) and sporangia.

FIG. 2. Sorus in transverse section showing central pillar and sporangia with annuli.

FIGS. 3–6. MATONIDIUM AMERICANUM Berry

FIG. 3. Two pinnules of normal form from below to show form and position of sori, × 10.

FIG. 4. Same in longitudinal vertical section, × 10.

FIG. 5. A single pinnule in transverse section showing sori and revolute margins, × 10.

FIG. 6. Two pinnules of the large form with maximum number of sori, from below, × 10.

Phytogeographical notes on the Rocky Mountain region VIII. Distribution of the Montane plants

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The Montane Zone or Pine Belt of the Rocky Mountain region includes approximately the areas between the altitudes of 2,500 and 3,000 m. in southern Colorado, between 1,800 and 2,500 m. in southern Montana, and between 1,200 and 1,800 m. in Alberta, where the Canadian Pacific Railroad crosses the mountains. A general description of the Zone has been given in a previous article.*

The Subalpine Zone of the Rockies comes in contact with the Hudsonian or Eastern Subarctic Zone along the foothills of the Rockies from the headwaters of the Peace River northward, and here the species of the East and of the Rockies more or less intermingle. But the relation between the Montane Zone of the Rockies and the Canadian or Eastern Boreal Zone is very different, for the latter, in its typical development, reaches its western limits in the region of the Lake of the Woods and Lake Winnipeg. The most representative species of the Canadian Zone, *Strobus Strobus* and *Pinus resinosa*, reach their northwestern limits in this region and it is only in the transition belt between the Canadian and Hudsonian Zones, which extends along the height of land between the Saskatchewan and Athabasca Rivers, that species of the Canadian Zone range farther west. This transition belt is characterized by mixed woods of *Pinus Banksiana*, belonging to the Canadian, and of spruces and larches belonging to the Hudsonian Zone. North of the upper Athabasca River and Beaver River practically the whole country is Hudsonian, while south of the northern branch of the Saskatchewan the prairies and the plains begin. These latter grassland formations belong to the Transition or Sub-boreal Zone.

The number of plants common to the Canadian Zone of the East and the Montane Zone of the Rockies is small, outside of

* See Bull. Torrey Club 42: 11–25. 1915.

the common transcontinental species that grow along the water-courses and species which are common to the Hudsonian-Subalpine Zone and the Canadian-Montane Zone. None of the conifers are common to the two regions, and among the trees which occur in common we find only a few species of *Salix*, *Populus*, and *Betula*. If we consider the relationship between the Montane plants of the Rockies and those of the Pacific Coast Mountains, however, we find the conditions quite different. The Cascade Mountains are directly connected with the Rockies in the north and there are several mountain chains interposed between the Cascades and the Rockies in British Columbia, separated from one another only by narrow river-valleys. The Montane Zone of the Cascades, therefore, is practically continuous with that of the Rocky Mountains, and the two regions have many plants in common, the leading conifers not excluded. Many of the Pacific species have emigrated into the Rocky Mountains, especially into the northern Rockies, and many Rocky Mountain species into the Cascades.

As has already been pointed out in earlier articles of mine, the Rockies may be divided into two principal parts, the Northern Rockies, extending from the Yukon Territory to northern Wyoming, and the Southern Rockies, of southern Wyoming, Colorado and northern New Mexico. Each of these main divisions may be subdivided, and the following districts may be distinguished:

Northern Rockies
1. Canadian Rockies
2. Main Range, Montana
3. Selkirk-Bitterroot District
4. Belt Mountains District
5. Yellowstone District
6. Sawtooth District
7. Big Horn District
8. Black Hills District

Southern Rockies
9. Main Range District
10. Uintah-Wasatch District
11. Sevier District
12. La Sal-Abajo District

The main range of the Northern Rockies north of Butte, Montana, is rather homogeneous and the change in the Montane flora seen in proceeding northward is rather gradual, although many of the high northern species found in the Canadian Rockies (District 1) are not found in Montana.

South of Butte the main range (District 2) becomes lower and less distinctly Montane until the neighborhood of Yellowstone Park is reached. Here it rises higher and the Alpine Zone is present in the Bear Tooth, Shoshone, Teton, Gros Ventre, and

Wind River Ranges. This region may be regarded as a distinct subdivision (District 5).

Numerous species belonging to the Cascade Mountains have invaded the Selkirk Mountains in British Columbia and the Bitter-root Mountains between Idaho and Montana, and the flora here has become more or less Pacific in its character. This region (District 3) includes also more or less the western slopes of the main range in British Columbia and northern Montana.

The mountains of Central Idaho, such as the Sawtooth, Salmon River, and other ranges (District 6) are characterized in the Montane Zone rather by the lack of many species found in the main range than by the introduction of any considerable new element. In the Submontane Zone, however, the character of the flora apparently is more like that of the mountains of the Great Basin than that of the main range, although the flora of this region is not so well known as might be desired.

The isolated mountains of central Montana, such as the Belt Mountains, the Snowy Mountains, the Crazy Mountains, and the Little Rocky Mountains, together with the Cypress Hills in Canada (District 4), being rather low, are characterized by a meagre Montane flora without any additional element. This can also be said of the Big Horn Mountains of Wyoming (District 7), although these are much higher and contain a few strictly endemic species.

The Black Hills of South Dakota and Wyoming are also to be counted as a subdivision of the Northern Rockies (District 8), although they contain quite a number of species belonging to the Southern Rockies as well as many belonging to the Canadian and Alleghanian Zones.

In the Southern Rockies the main range (District 9) includes all of the mountains in Colorado and northern New Mexico, together with the Sierra Madre, Medicine Bow, and Laramie Ranges in Wyoming. Only a few peaks of the latter reach the Montane Zone.

The Uintah and the northern part of the Wasatch Mountains in Utah (District 10), although geologically belonging to the Northern Rockies, have a flora closely resembling that of the Southern Rockies. In the Wasatch Mountains, however, there

are found quite a number of species which have immigrated from the Northern Rockies or from the mountains of the Great Basin. The southern part of the Wasatch Mountains, including the Sevier Range, the Henry Mountains, and other ranges west of the Colorado of the West (District 11), have a flora characteristic of the Basin Mountains. The Montane flora consists to a great extent of species common to the Rockies, the Basin Mountains, and the Sierra Nevada. The La Sal and Abajo Mountains, in Southeastern Utah (District 12) have a mountain flora almost the same as that characteristic of the main range of the Southern Rockies in Colorado.

The plants of the Montane Zone of the Rocky Mountains may be classified in the following categories. These are practically the same as those in the Subalpine Zone, with, however, some modification.

I. Transcontinental Species.
II. Species common to the Rockies and the Canadian Zone of the East.
III. Species common to the Rockies and the Pacific Mountains.
IV. Endemic species.

I. Transcontinental Species

The transcontinental species, as well as most of those common to the Rockies and to the East, consist partly of forest species, most of which have migrated around the Saskatchewan Plains, partly of water, meadow, and thicket species which have followed the watercourses across the plains. The former consist to a great extent of species common to the Subalpine and Montane Zones in the Rockies and hence also to the Hudsonian and Canadian Zones of the East; the latter consist mostly of species found also in the Submontane and Transition (or Alleghanian) Zones. Many of the water and bog plants, however, are not found on the plains and hence must have followed the woods.

A. TRANSCONTINENTAL SPECIES RANGING THROUGHOUT THE ROCKIES

Here I have included species which are found in the main ranges of both the Northern and Southern Rockies. Many of

these may be lacking in one or more of the districts or subdivisions, especially in Districts 8, 11, and 12, but some also in Districts 4, 6, and 7.

1. PLANTS WITH BOREAL-SYLVAN DISTRIBUTION

In this discussion the word "sylvan" applied to a plant does not mean that it grows only in the deep woods, but that its distribution has taken place in connection with the Northern Woods, and that it does not grow in the prairie or plains regions. The plant may be a forest species in the true sense or it may grow in open woods, thickets, or among rocks in more open places. The essential point is that its migration east or west has taken place around and north of the plains, and not across them along the watercourses. To this category belong the transcontinental trees and most of the shrubs. The most important of the former is the quaking aspen, *Populus tremuloides*, also found in the Subalpine Zone.

In this and subsequent lists, species which are marked "**" are rare in the Southern Rockies; those marked "†" attain their best development at higher altitudes and reach the Alpine zone; those marked "‡" develop best lower down and reach the plains; those followed by "(Eur.)" are found also in Europe and usually also in northern Asia. The nomenclature is that of the author's Flora.*

a. Forest species

Trees

Populus tremuloides
*Populus balsamifera***
Salix Bebbiana
*Betula papyrifera***

Shrubs

Juniperus sibirica (Eur.)
Dasiphora fruticosa (Eur.)
Chamaepericlymenum candense
Lepargyraea canadensis
Arctostaphylos Uva-ursi (Eur.)
Linnaea americana
Distegia involucrata

* Flora of The Rocky Mountains and Adjacent Plains. New York. 1917.

Herbs

Phleum alpinum (Eur.)
Avena striata
Danthonia spicata
Poa compressa (Eur.)
Allium sibiricum (Asia)
Lysiella obtusata
Peramium decipiens
Cytherea bulbosa (Eur.)
Corallorrhiza multiflora
Tium alpinum (Eur.)
Chamaenerium spicatum (Eur.)
Heracleum lanatum
Moneses uniflora (Eur.)
Pyrola uliginosa
*Pyrola asarifolia***
Pyrola chlorantha (Eur.)
Pyrola elliptica
Erxlebenia minor (Eur.)
Ramischia secunda (Eur.)
Monotropa uniflora
Veronica serpyllifolia (Eur.)
Galium boreale (Eur.)
Galium triflorum
Specularia perfoliata
Botrychium Lunaria (Eur.)
Botrychium virginianum (Eur.)
*Botrychium silaifolium***
Filix bulbifera
Filix fragilis (Eur.)
Filix montana (Eur.)
Polystichum Lonchitis
Thelypteris Dryopteris (Eur.)
Asplenium septentrionale (Eur.)
Asplenium Trichomanes (Eur.)
Pteris aquilina (Eur.)
Cryptogramma acrostichoides

b. Aquatic and bog species

The following water and bog plants probably reached the Rockies by the way of the Northern Woods:

Shrubs

Salix chlorophylla
Betula glandulosa

Herbs

Sparganium minimum (Eur.)
Triglochin palustris (Eur.)
Calamagrostis Langsdorfii (Eur.)
Deschampsia caespitosa
Catabrosa aquatica (Eur.)
Panicularia nervata
Panicularia borealis
Panicularia septentrionalis
Eriophorum angustifolium (Eur.)
Scirpus pauciflorus (Eur.)
Scirpus caespitosus (Eur.)
Carex diandra (Eur.)†
Carex gynocrates (Eur.)
Carex disperma (Eur.)
Carex canescens (Eur.)
Carex brunnescens (Eur.)
Carex paupercula (Eur.)
Carex aquatilis (Eur.)
Bistorta vivipara (Eur.)†
Alsine borealis

Sagina saginoides (Eur.)
Thalictrum alpinum (Eur.)†
Batrachium flaccidum (Eur.)
Ranunculus reptans
Cardamine pennsylvanica
Subularia aquatica (Eur.)
Epilobium alpinum (Eur.)†
Epilobium Hornemannii (Eur.)†
Mimulus moschatus
Limosella aquatica (Eur.)
Limosella tenuifolia (Eur.)
Veronica Wormskjoldii†
Elephantella groenlandica
Senecio pauciflorus
Lycopodium annotinum (Eur.)

c. Various mesophytes

A few plants which are neither aquatics nor forest species have invaded the Rockies from the north. These are species that grow among bushes, among rocks, or on hillsides.

Torresia odorata (Eur.)
Calamagrostis purpurascens
Poa crocata
Festuca rubra (Eur.)
Bromus ciliatus
Carex praticola
Carex concinna
Carex Halleri (Eur.)
Juncoides parviflorum (Eur.)
Juncoides intermedium
Juncoides spicatum (Eur.)†
Blitum capitatum (Eur.)
Moehringia latifolia (Eur.)
Moehringia macrophylla
Viola adunca

2. PLANTS WITH RIPARIAN OR CAMPESTRIAN DISTRIBUTION

These plants have crossed the continent over the plains, following mostly the watercourses. All of them are found in the foothills also and most of them attain their best development on the plains and prairies.

a. Aquatic plants

Sparganium angustifolium‡
Potamogeton natans (Eur.)‡
Potamogeton alpinus (Eur.)‡
Potamogeton lucens (Eur.)‡
Potamogeton foliosus‡
Triglochin maritima (Eur.)
Alisma brevipes
Sagittaria latifolia‡
Phragmites Phragmites (Eur.)‡
Panicularia grandis‡
Eleocharis palustris (Eur.)‡
Eleocharis acicularis (Eur.)‡
Eriophorum gracile (Eur.)‡
Scirpus validus‡
Lemna trisulca (Eur.)‡
Lemna minor (Eur.)‡
Persicaria coccinea‡
Batrachium trichophyllum (Eur.)‡

Batrachium Drouetii (Eur.)‡
Ranunculus Purshii‡
Sisymbrium Nasturtium-aquaticum (Eur.)‡
Tillaeastrum aquaticum (Eur.)‡
Callitriche palustris (Eur.)‡
Callitriche autumnalis (Eur.)‡
Hippuris vulgaris (Eur.)‡
Sium cicutaefolium‡
Menyanthes trifoliata (Eur.)‡
Veronica americana‡
Utricularia vulgaris (Eur.)‡
Utricularia minor (Eur.)‡

b. Bog and wet meadow plants

Tree

Salix cordata

Herbs

Phalaris arundinacea (Eur.)‡
Alopecurus aristulatus‡
Calamagrostis elongata‡
Calamagrostis canadensis‡
Beckmannia erucaeformis‡
Carex leptalea (Eur.)
Carex aurea‡
Carex Buxbaumii (Eur.)‡
Carex lanuginosa
Carex viridula‡
Carex rostrata‡
Carex retrorsa‡
Rumex occidentalis
Rumex mexicanus
Ranunculus sceleratus (Eur.)
Halerpestes Cymbalaria‡
Argentina Anserina (Eur.)‡
Gnaphalium uliginosum (Eur.)
Equisetum arvense (Eur.)

c. Meadow plants

Agrostis hyemalis‡
Muhlenbergia Richardsonis
Poa annua (Eur.)‡
Poa triflora (Eur.)‡
Poa pratensis (Eur.)‡
Festuca octoflora‡
Hordeum jubatum‡
Carex stenophylla‡
Carex interior
Juncus bufonius (Eur.)‡
Polygonum ramosissimum‡
Capnodes aureum‡
Arabis ovata‡
Draba nemorosa‡
Viola nephrophylla‡
Viola septentrionalis‡
Artemisia biennis

To this category belong also some of the escaped cultivated plants and common weeds, such as

Phleum pratense (Eur.)‡
Dactylis glomerata (Eur.)‡
Syntherisma Ischaemum (Eur.)
Chenopodium Botrys (Eur.)‡
Bursa Bursa-pastoris (Eur.)‡
Carum Carui (Eur.)‡
Plantago major (Eur.)‡

d. Hillside plants

Panicum Huachucae
Ibidium strictum
Polygonum Douglasii
Bilderdykia Convolvulus (Eur.)
Pulsatilla ludoviciana

B. TRANSCONTINENTAL SPECIES RESTRICTED TO THE NORTHERN ROCKIES

Nearly all of the transcontinental plants restricted in their distribution to the Northern Rockies are of boreal-sylvan distribution, whether they are forest species or not. In spreading across the continent, they have followed the northern woods around the plains north of the Saskatchewan and then south in the mountains. In some cases the species have not extended very far south—have not even entered the United States; in other words, their distribution in the Rockies is limited to District 1, the Canadian Rockies. Others have traveled farther south and invaded District 2, or even Districts 3 and 4. About one third have spread further south into District 5 and from there to Districts 6, 7 and 8. Two are even found in the Uintah-Wasatch District of the Southern Rockies.

1. SPECIES REACHING AT LEAST THE YELLOWSTONE DISTRICT

a. Forest plants

Sabina horizontalis
Melica Smithii
Oryzopsis pungens
Carex Peckii
Streptopus amplexifolius
Rosa acicularis (Asia)
Osmorrhiza divaricata
Androsace septentrionalis (Eur.)
Valeriana septentrionalis
Aster major
Aster Lindleyanus
Youngia nana (Asia)†
Aspidium viride (Eur.)

b. Water and bog plants

Eriophorum Scheuchzeri (Eur.)†
Eriophorum Chamissonis (Eur.)†
Carex livida
Juncus Richardsonianus
Comarum palustre (Eur.)
Equisetum palustre (Eur.)
Equisetum fluviatile
Equisetum laevigatum

c. Cliff plant

Antiphylla oppositifolia (Eur.)†

Of these species *Oryzopsis pungens*, *Carex Peckii*, *Osmorrhiza divaricata* and *Juncus Richardsonianus* have extended their range into the Black Hills of South Dakota, and *Osmorrhiza divaricata* and *Youngia nana* into the Uintah Mountains of Utah.

2. Species reaching the Main Range in Montana or the Bitter-roots in Idaho, but not further south

a. Forest plants

Actaea rubra
Ribes Hudsonianum
Dryopteris Filix-mas (Eur.)
Dryopteris dilatata (Eur.)
Lycopodium obscurum (Eur.)
Lycopodium complanatum (Eur.)
Lycopodium clavatum (Eur.)
Lycopodium sitchense

b. Water and bog plants

Shrubs

Salix pedicellaris
Salix candida

Herbs

Rynchospora alba (Eur.)
Scirpus subterminalis
Scirpus atrocinctus
Carex vaginata (Eur.)
Carex limosa (Eur.)
Carex scirpoidea (Eur.)
Carex lacustris (Eur.)
Carex Crawfordii
Carex flava (Eur.)
Castalia Leibergii
Drosera rotundifolia (Eur.)
Drosera longifolia (Eur.)
Geum macrophyllum
Mertensia paniculata
Equisetum sylvaticum (Eur.)
Equisetum scirpoides (Eur.)
Lycopodium inundatum (Eur.)

Pellaea glabella, growing among exposed rocks, has a peculiar distribution. Though it is not found in the Southern Rockies it is found in the Black Hills and the hilly country of western Nebraska and reappears in eastern Kansas.

3. SPECIES LIMITED TO THE CANADIAN ROCKIES

a. Forest species

Carex aenea
Carex durifolia
Cypripedium passerinum
Lysias orbiculata
Ophrys convallarioides
Comandra livida
Coptis trifoliata (Eur.)
Thelypteris Phegopteris (Eur.)
Dryopteris fragrans (Eur.)
Woodsia glabella (Eur.)
Lycopodium alpinum (Eur.)

b. Water and bog plants

Herbs

Eriophorum callitrix (Eur.)
Eriophorum opacum (Eur.)
Scirpus pumilus†
Carex chordorrhiza
Carex militaris
Carex deflexa
Oxycoccus Oxycoccus (Eur.)
Oxycoccus macrocarpus

II. Species common to the Rockies and the Canadian Zone

The plants common to the Rockies and to the Canadian Zone of the East consist either of eastern species, whose ranges extend west into the Rockies, or of Rocky Mountain species which have invaded the East. The distribution of the former in the Rockies is very similar to that of the transcontinental species just treated. Some of them have followed the northern woods, others the watercourses across the plains. The distribution area of some reaches the Southern Rockies, while that of others stops in northern Wyoming, in northern Montana, or in the Canadian Rockies. Among the Rocky Mountain species which have emigrated east, some have reached the Lake Superior region, while others are found as far east as the Gaspé Peninsula of Quebec.

A. EASTERN SPECIES, EXTENDING SOUTH INTO THE SOUTHERN ROCKIES

1. Plants of boreal-sylvan distribution

a. Forest species

Oryzopsis asperifolia
Agrostis oreophila
Cinna latifolia (Eur.)
Carex Parryana†
Vagnera stellata
Coeloglossum bracteatum
Peramium ophioides
Corallorrhiza Corallorrhiza (Eur.)

Claytonia virginica
Ranunculus micranthus
Fragaria americana
Rubus pubescens
Viola Selkirkii
Viola renifolia
Viola canadensis
Circaea alpina (Eur.)
Aralia nudicaulis
Prunella vulgaris (Eur.)
Clinopodium vulgare (Eur.)
Pedicularis canadensis
Linnaea americana
Erigeron droebachiensis (Eur.)
Botrychium simplex (Eur.)
Botrychium neglectum (Eur.)
Cryptogramma Stelleri
Selaginella selaginoides

b. Water and bog plants

Alsine alpestris (Eur.)
Alsine crassifolia
Parnassia parviflora
Geum rivale (Eur.)
Viola palustris (Eur.)
Epilobium adenocaulon
Petasites sagittata
Nabalus racemosa
Lactuca spicata
Equisetum pratense (Eur.)

2. EASTERN PLANTS WITH RIPARIAN OR CAMPESTRIAN DISTRIBUTION

Muhlenbergia racemosa
Juncus Vaseyi
Carex lanuginosa
Urtica gracilis
Carex siccata
Thalictrum dasycarpum
Lepidium densiflorum†
Sullivantia Hapemanii
Vicia trifida
Vicia americana
Apocynum androsaemifolium
Macrocalyx Nyctelea‡
Plantago eriopoda‡
Rudbeckia hirta

Vitis riparia, *Juncus Torreyi*, and *Asplenium platyneuron*, eastern species, have reached the Southern Rockies in Colorado, but are not found in the Northern.

3. PLANTS OF THE GREAT PLAINS

Some of the plants of the Great Plains extend up into the Montane Zone. Although they do not belong to the Canadian or Alleghanian Zones of the eastern United States, they are immigrants from the East and may be included here.

Calamagrostis micrantha
Polygonum buxiforme
Xanthoxalis Bushii
Viola pedatifida
Anogra latifolia
Anogra coronopifolia
Plantago Purshii
Laciniaria punctata
Chrysopsis villosa
Solidago glaberrima
Equisetum variegatum

B. Eastern species, extending into the Northern Rockies only

1. Species reaching at least the Yellowstone Region

Carex Richardsonii
Carex eburnea
Heuchera hispida
Phaca americana
Hedysarum americanum

Of these, *Heuchera hispida* and *Phaca americana* even reach the Black Hills and western Nebraska.

2. Species extending only to Northern Montana or Idaho

Carex tenera
Carex pedunculata
Parnassia palustris (Eur.)
Mitella nuda
Chiogenes hispidula
Melampyrum lineare
Thelypteris Robertiana (Eur.)
Dryopteris cristata (Eur.)

3. Species limited to the Canadian Rockies

Trees

Picea canadensis
Picea mariana

Shrub

Salix pellita

Herbs

Carex atratiformis
Vagnera trifoliata
Coptidium lapponicum (Eur.)
Ribes glandulosum
Geum perincisum
Primula mistassinica
Petasites palmata
Pteretis nodulosa
Dryopteris intermedia

Of these, *Picea canadensis* and *Pteretis nodulosa* are found also in the Black Hills.

C. Rocky Mountain species which have emigrated eastward

The following plants have extended their ranges as far east as eastern Minnesota, western Ontario, upper Michigan or Hudson Bay.

Shrubs

Rosa Bourgeauiana
Amelanchier alnifolia

Herbs

Viola rugulosa
Monarda menthaefolia
Androsace subumbellata
Aster laevis
Aster Wilsonii
Solidago pulcherrima
Erigeron glabellus

Another species, *Dryas Drummondii*, has even reached the Gaspé Peninsula, Quebec.

III. Species common to the Rockies and the Pacific Mountains

A. Species found in both the Northern and Southern Rockies, as well as the Cascades and the Sierras

a. Forest species

Nearly all of the plants belonging in this category have passed from the Rockies to the Pacific Mountains, or vice versa, in the north where the two mountain systems are connected, and not across the Great Basin.

Trees

Pseudotsuga mucronata
Pinus Murrayana
Apinus flexilis
Salix Scouleriana

Shrubs

Odostemon Aquifolium
Ribes viscosissimum
Rubacer parviflorum
Echinopanax horridum
Pachystima Myrsinites
Gaultheria humifusa
Vaccinium scoparium

Herbs

Oryzopsis Bloomeri
Festuca subulata
Elymus glaucus
Carex Bolanderi
Carex athrostachya
Veratrum speciosum
Vagnera amplexicaulis
Vagnera lilacina
Trillium ovatum
Piperia unalaschensis
Ranunculus Douglasii
Ranunculus Bongardii
Actaea arguta
Thalictrum sparsiflorum
Aquilegia coerulea
Osmorrhiza obtusa
Pectianthia pentandra
Fragaria bracteata
Geranium viscosissimum
Geranium Richardsonii

Linum Lewisii
*Circaea pacifica**
Glycosma occidentalis
Chimaphila occidentalis
Pyrola picta
Pterospora Andromedea
Androsace filiformis (Asia)
Polemonium occidentale
Collinsia parviflora
Pedicularis racemosa
Achillea lanulosa
Artemisia frigida (Asia)
Arnica cordifolia
Senecio pseudaureus
Hieracium albiflorum
Athyrium alpestre (Eur.)
Athyrium cyclosorum (Eur.)
Cryptogramma densa
Polypodium hesperium

Cryptogramma densa, *Athyrium alpestre*, and *Osmorrhiza obtusa* reappear eastward on the Gaspé Peninsula, Quebec. When their distribution in Canada becomes better known, they may prove to belong among the transcontinental plants. *Thalictrum sparsiflorum* extends east to the Hudson Bay, *Elymus glaucus* to Upper Michigan, and *Collinsia parviflora* and *Achillea lanulosa* to western Ontario; *Echinopanax horridum* is found near the shores of Lake Superior.

b. Water and bog plants

In this class have also been included many plants of the wetter meadows and copses; in other words, the class consists of plants which probably have spread along the watercourses. This means, in this case, mostly along the Columbia River and its tributaries, for the Frazer River drains mostly the Cascades and other ranges west of the Rockies. Only the headwaters of this stream are in the Rocky Mountains, though north of the region here considered and mainly within the Subarctic Zone. The Colorado of the West runs for hundreds of miles in a deep canyon, does not touch the Sierras, and therefore can play practically no part in the distribution of the Montane plants.

Shrubs

Salix glaucops
Alnus tenuifolia
Kalmia microphylla

Herbs

Muhlenbergia comata‡
Muhlenbergia filiformis
Agrostis grandis
Agrostis asperifolia‡

Agrostis variabilis
Graphephorum Brandegei
Danthonia californica
Danthonia unispicata
Carex Raynoldsii
Carex tenuirostris
Carex simulata
Carex athrostachya
Carex Kelloggii
Lemna gibba (Eur.)
Juncus Mertensianus
Iris missouriensis
Polygonum Watsonii
Bistorta bistortoides†
Claytonia lanceolata
Crunocallis Chamissonis
Alsine strictiflora
Alsine laeta†
Alsine calycantha
Nymphaea polysepala
Thalictrum sparsiflorum (Asia)
Myosurus aristatus
Ranunculus Eschscholtzii
Campe americana‡
Parnassia fimbriata
Micranthes arguta
Geum oregonense
Vicia oregana‡
Vicia sparsiflora‡
Epilobium brevistylum
Epilobium occidentale
Amarella strictiflora
Mimulus Langsdorfii
Mimulus Lewisii‡
Pedicularis bracteosa
Galium subbiflorum
Aster occidentalis
Aster Burkei
Erigeron salsuginosus
Rudbeckia occidentalis
Senecio triangularis
Arnica longifolia
Agoseris elata

Of these, some have spread also to the East, as *Crunocallis Chamissonis* and *Galium subbiflorum* to Minnesota, *Linum Lewisii* to the Black Hills and Nebraska, *Alsine strictiflora* to Ontario, and *Thalictrum sparsiflorum* and *Alsine laeta* to Hudson Bay.

c. Various mesophytes

In this category are included plants that grow in open places, as dry meadows, table-land, hillsides and cliffs. Many of these grow also at lower altitudes; in the foothills and even on the plains. Many are also common to the mountain chains of the Great Basin.

Trees or shrubs

Cercocarpus ledifolius
Limnobotrya montigena

Herbs

Eriocoma hymenoides‡
Poa longiligula
Poa Sandbergii
Hesperochloa Kingii‡
Agropyron Smithii‡
Elymus condensatus‡
Carex Douglasii‡
Carex Hoodii
Carex phaeocephala†
Carex obtusata (Eur.)
Carex Rossii
Juncus longistylis
Juncoides comosum
Eriogonum stellatum
Eriogonum umbellatum
Eriogonum ovalifolum
Polygonum sawatchense
Sarcobatus vermiculatus‡
Eurotia lanata‡
Lewisia redeviva
Oreobroma pygmaea
Cerastium strictum (Eur.)
Arenaria congesta†
Arenaria Burkei‡
Anemone globosa
Draba lutea (Eur.)
Arabis retrofracta
Sedum stenosepalum
Lithophragma bulbifera
Lithophragma parviflora
Petrophytum caespitosum
Potentilla Bakeri
Potentilla diversifolia
Drymocallis glandulosa
Lupinus tenellus
Lupinus argenteus‡
Viola venosa
Viola linguaefolia
Epilobium paniculatum‡
Gayophytum intermedium
Gayophytum ramosissimum
Gayophytum racemosum
Oenothera Hookeri
Lavauxia flava
Leptodactylon pungens
Leptodactylon Nutallii
Gilia aggregata
Collomia linearis
Hydrophyllum capitatum
Lappula floribunda
Cryptantha Torreyana
Pentstemon procerus
Castilleja linariaefolia
Campanula petiolata
Macronema suffruticosum
Aster campestris
Antennaria rosea
Antennaria oblanceolata
Gymnolomia multiflora‡
Balsamorrhiza sagittata
Wyethia amplexicaulis
Helianthus petiolaris‡
Madia glomerata
Chaenactis Douglasii
Artemisia incompta
Artemisia tridentata‡
Arnica pedunculata
Arnica fulgens
Agoseris laciniata
Woodsia oregana
Woodsia scopulina

Of these *Eriocoma hymenoides*, *Juncus longistylis*, *Arabis retrofracta*, *Lithophragma bulbifera*, *L. parviflora*, *Petrophytum caespitosum*, *Drymocallis glandulosa*, *Epilobium paniculatum*, *Arnica pedunculata*, and *A. fulgens* extend as far east as South Dakota and Nebraska; *Gilia aggregata* extends to Minnesota, reappearing farther east on the Gaspé Peninsula; *Carex Rossii* and *Draba lutea* to upper Michigan; *Woodsia scopulina* and *W. oregana* are found on the Gaspé Peninsula.

B. ROCKY MOUNTAIN SPECIES FOUND IN BOTH SOUTHERN AND NORTHERN ROCKIES, WHICH HAVE SPREAD INTO THE CASCADES, BUT ARE NOT FOUND IN SIERRA NEVADA

a. Forest species

Tree

Picea Engelmannii

Shrubs

Sorbus scopulina
Rubus melanolasius

Herbs

Calamagrostis luxurians
Carex Geyeri
Ophrys nephrophylla
Razoumofskia americana
Razoumofskia Douglasii
Atragene columbiana
Ozomelis stauropetala
Conioselinum scopulorum
Ligusticum tenuifolium
Apocynum ambigens
Aster Geyeri
Erigeron macranthus
Erigeron speciosus
Erigeron conspicuus

b. Water and bog plants

Shrub

Salix exigua

Herbs

Poa leptocoma
Poa interior
Poa Olneyæ
Agrostis humilis
Agrostis idahoensis
Limnorchis stricta
Limnorchis borealis
Limnorchis viridiflora
Ibidium porrifolium
Alsine obtusa
Ranunculus alismaefolius
Ranunculus cardiophyllus‡
Trollius albiflorus
Delphinium multiflorum
Argentina argentea
Dodecatheon parviflorum
Castilleja exilis
Graphalium sulphurescens

Of these *Argentina argentea* extends east to South Dakota and *Ranunculus cardiophyllus* to eastern Saskatchewan.

c. Various mesophytes

Melica spectabilis
Melica bella
Bromus polyanthus
Carex nubicola
Carex pachystachya
Carex Geyeri
Carex filifolia‡
Carex scopulorum
Anticlea elegans
Juncus confusus
Allium Geyeri
Delphinium Nelsonii
Thlaspi Nuttallii
Draba nitida
Peritoma serrulatum
Leptasea austromontana
Potentilla Nuttallii
Drymocallis corymbosa
Sieversia grisea
Sieversia ciliata
Thermopsis montana
Lupinus caespitosus
Astragalus striatus
Astragalus goniatus
Viola vallicola
Phlox caespitosa
Gilia pulchella
Phacelia sericea
Castilleja lancifolia
Castilleja lauta
Castilleja hispida
Orthocarpus luteus
Coleosanthus grandiflorus
Aster apricus
Antennaria flavescens
Antennaria concinna
Atnennaria corymbosa
Antennaria pulcherrima
Antennaria anaphaloides
Artemisia Michauxiana
Artemisia cana‡
Artemisia arbuscula
Artemisia tripartita
Arnica Parryi
Arnica mollis
Arnica Rydbergii
Senecio serra
Selaginella densa

Of these, *Delphinium Nelsonii, Anticlea elegans, Juncus confusus*, and *Allium Geyeri* extend east to South Dakota or Nebraska, *Astragalus striatus* to Minnesota, and *A. goniatus* to Hudson Bay.

c. Pacific species, which have invaded the Northern Rockies, but not the Southern

1. Species which have reached only the Selkirk-Bitterroot District

a. Forest species

The species listed here have probably followed the mountain chains in their migration from the Pacific Mountains by the way of the Cascades and the Selkirks into the Rockies.

Trees

Strobus monticola
Larix occidentalis
Abies grandis
Tsuga heterophylla
Thuja plicata
Taxus brevifolia

Shrubs

Ribes nevadense
Rubus nivalis
Rubus spectabilis
Ceanothus prostratus
Azaliastrum albiflorum
Vaccinium parvifolium
Linnaea longiflora

Herbs

Carex laeviculmis
Unifolium dilatatum
Allium validum
Disporum oreganum
Clintonia uniflora
Piperia multiflora
Piperia elegans
Lysias Menziesii
Eburophyton Austinae
Cytherea occidentalis
Corallorrhiza Mertensiana
Trautvetteria grandis
Mitellastra caulescens
Pectianthia Breweri
Therophon majus
Chimaphila Menziesii
Castilleja pinetorum

b. Water and bog plants

These have probably followed the Columbia River and Frazer River and their tributaries up into the mountains.

Shrubs or trees

Salix Lemmoni
Salix sitchensis

Herbs

Agrostis foliosa
Calamagrostis Cusickii
Graphephorum muticum
Tofieldia occidentalis
Cardamine oligosperma
Lupinus polyphyllus
Trifolium longipes
Epilobum oregonense
Epilobum glaberrimum
Dodecatheon Jeffreyi
Anthopogon simplex
Mimulus nasutus
Mimulus primuloides
Mimulus Breweri
Polystichum munitum
Isoetes Howellii
Isoetes Nuttallii

C. Various mesophytes

These have probably spread along the foothills from the Cascades to the Selkirks and Bitterroots, or even across the Columbia Plains, as most of them are also found in the Submontane or Transition Zone.

Herbs

Stipa Thurberiana
Festuca viridula
Hordeum murinum (Eur.)
Carex concinnoides
Carex spectabilis
Carex Mertensii
Eriogonum pyrolaefolium
Delphinium depauperatum
Pulsatilla occidentalis
Arabis suffrutescens
Phoenocaulis cheiranthoides
Sedum Douglasii
Heterisia Mertensiana
Dasystephana oregana
Stenotus stenophyllus
Antennaria confinis
Balsamorrhiza deltoidea
Arnica Menziesii
Cheilanthes gracillima
Selaginella Wallacei

2. SPECIES WHICH HAVE CROSSED THE MAIN RANGE OF THE ROCKIES IN MONTANA AND ALBERTA

a. Forest species

Trees

Pinus ponderosa
Apinus albicaulis

Shrubs

Ribes laxiflorum
Rubus pedatus
Acer Douglasii

Herbs

Melica subulata
Aquilegia formosa
Tiarella unifoliata
Adenocaulon bicolor
Pyrola dentata

b. Water and bog plants

Poa nervosa
Naiocrene parvifolia
Viola Macloskeyi
Trifolium Beckwithii

c. Various mesophytes

Carex Preslii
Xerophyllum tenax
Anemone Drummondii
Smelowskia ovalis
Arabis Lyallii
Lupinus laxiflorus
Phlox Douglasii
Pedicularis contorta
Arnica diversifolia

Adenocoulon bicolor reappears on Lake Superior and *Trifolium Beckwithii* in eastern South Dakota.

3. SPECIES WHICH HAVE REACHED THE YELLOWSTONE PARK

a. Forest species

Calamagrostis Suksdorfii
Hypericum Scouleri
Ozmorrhiza brevipes
Kelloggia galioides
Aster integrifolius
Antennaria racemosa

b. Bog plants

Shrub

Salix Austinae

Herbs

Panicum thermale
Tofieldia intermedia
Juncus nevadensis
Alsine crispa
Ranunculus alismellus
Cardamine Breweri

c. Mesophytes

Stipa Elmeri
Stipa oregonensis
Calamagrostis rubescens
Carex Jonesii
Carex nervina
Carex luzulina
Potentilla Blaschkeana
Potentilla glomerata
Fragaria platypetala
Dasystephana calycosa
Townsendia scapigera‡
Balsamorrhiza terebinthacea‡

4. SPECIES WHOSE DISTRIBUTION EXTENDS EVEN INTO THE UINTAH AND WASATCH MOUNTAINS OF UTAH

a. Forest species

Shrubs

Vaccinium occidentale
Sambucus coerulea

Herbs

Aquilegia flavescens
Bicuculla uniflora
Apocynum pumilum

b. Water and bog plants

Shrub

Ledum glandulosum

Herbs

Ruppia pectinata
Limnia asarifolia
Limnia sibirica (Asia)
Limnia perfoliata
Alsinopsis occidentalis
Alsine brachypetala
Dodecatheon alpinum
Aster oreganus

c. Mesophytes

Agrostis Thurberiana
Arenaria Douglasii
Thalictrum occidentale
Paeonia Brownii
Thlaspi californicum
Draba oligosperma
Arabis Lemmonii
Lupinus leucophyllus
Gayophytum diffusum
Gayophytum pumilum
Lappula diffusa

D. PLANTS COMMON TO THE NORTHERN ROCKIES AND THE CASCADES, BUT NOT FOUND IN THE SOUTHERN ROCKIES OR IN SIERRA NEVADA

1. SPECIES FOUND AS FAR SOUTH AS THE YELLOWSTONE PARK REGION

a. Forest shrubs

Spiraea densiflora
Spiraea lucida
Menziesia ferruginea
Menziesia glabella

b. Bog plants

Shrubs

Salix idahoensis
Salix Geyeriana
Alnus sinuata

Herbs

Agrostis oregonensis
Carex Piperi
Carex microptera
Caltha leptosepala
Lupinus Burkei
Epilobium delicatum
Angelica Lyallii
Dodecatheon conjugens
Aster Jessicae
Senecio subnudus
Botrychium Coulteri

c. Various mesophytes

Sitanion montaum
Elymus nitidus
Carex Tolmei
Eriogonum Piperi
Spraguea multiceps
Silene Lyallii
Silene oregana
Silene multicaulis
Thalictrum columbianum
Delphinium Nuttallianum
Arabis albertina
Lupinus leucopsis
Lupinus sericeus
Cordylophorum suffruticosum
Amarella anisosepala
Dasystephana monticola
Pentstemon crassifolius
Castilleja pallescens
Valeriana ceratophylla
Aster conspicuus
Antennaria flagellaris
Antennaria Howellii
Artemisia floccosa
Arnica gracilis
Senecio Howellii
Hieracium cynoglossoides

Lupinus sericeus and *Aster conspicuus* extend east to the Black Hills.

2. Species whose range extends even into the Uintah-Wasatch region

Juncus Regelii
Silene columbiana
Ranunculus limosus
Delphinium bicolor
Arabis rupestris
Arabis microphylla
Potentilla dichroa
Castilleja Tweedyi
Eucephalus elegans
Hieracium albertinum
Hieracium griseus
Gnaphalium proximum

3. SPECIES FOUND IN THE MAIN RANGE IN MONTANA AND ALBERTA BUT NOT FARTHER SOUTH

Shrubs

Salix Fernaldii
Philadelphus Lewisii
Ribes petiolare
Rosa nutkana
Sorbus occidentalis
Vaccinium globulare
Luetkea pectinata

Herbs

Poa Vaseyochloa
Xerophyllum Douglasii
Juncoides glabratum
Erythronium grandiflorum
Eriogonum polyphyllum
Eriogonum depressum
Arenaria nardifolia (Asia)
Silene repens (Asia)
Atragene grosseserrata
Arabis Nuttallii
Arabis furcata
Heuchera glabra
Heuchera grossulariifolia
Micranthes aestivalis
Potentilla Drummondii
Epilobium luteum
Viola orbiculata
Valeriana Scouleri
Penstemon Lyallii
Dodecatheon cylindrocarpum
Dodecatheon viviparum
Castilleja Suksdorfii
Castilleja lutea
Antennaria Howellii
Antennaria luzuloides
Erigeron Howellii
Aster modestus
Aster diabolicus
Aster Sayianus
Achillea fusca
Cirsium Macounii
Selaginella montanensis

4. CASCADE MOUNTAIN SPECIES WHICH HAVE EMIGRATED INTO THE SELKIRK-BITTERROOT REGION

Shrub

Salix commutata

Herbs

Alopecurus pallescens
Poa Cusickii
Agropyron lanceolatum
Elymus Howellii
Carex stenochlaena
Allium fibrillum
*Allium Cusickii**
Eriogonum thymoides
Claytonia chrysantha
Alsine washingtoniana
Arenaria cephaloidea
Aquilegia columbiana
Sedum Leibergii
Hemieva ranunculifolia

Aruncus acuminatus
Trifolium plumosum
Angelica Piperi
Osmorrhiza Leibergii
Osmorrhiza purpurea
Ligusticum Canbyi
Ligusticum Leibergii
Chamaepericlymenum unalaschense
Moneses reticulata
Pyrola bracteata
Oxycoccus intermedius
Pentstemon pinetorum
Veronica Cusickii
Synthyris major
Castilleja cervina
Razoumofskya Laricis
Valeriana sitchensis
Castilleja Vreelandii
Aster Cusickii
Balsamorrhiza Careyana
Saussurea americana
Lactuca multifida
Polystichum Andersoni
Thelypteris Oreopteris (Eur.)

E. Plants common to the Southern Rockies and the Sierra Nevada

These plants have spread across the Great Basin, their seed being carried by birds or wind from mountain to mountain by way of the numerous though low parallel mountain chains within the Basin. Most of them are xerophytic, the rest mesophytic. Species in the following list marked "††" extend into the Submontane Zone; those marked "‡‡" are not found east of the Wasatch Mountains.

Trees

Pinus aristata
Abies concolor

Herbs

Elymus simplex††
Stipa speciosa‡‡††
Oryzopsis Webberi††
Muhlenbergia gracilis††
Poa Fendleriana
Carex fissuricola‡‡
Carex epapillosa‡‡
Rumex hymenosepalus††
Amaranthus Powellii
Quamoclidion multiflorum††
Oreobroma nevadensis
Erocallis triphylla
Alsine Jamesii
Lepidium montanum††
Heuchera rubescens‡‡††
Sericotheca glabrescens‡‡††
Drymocallis pumila‡‡
Trifolium Rusbyi‡‡
Phaca Hookeriana‡‡††
Hamosa calycosa‡‡††
Kentrophyta tegetaria‡‡
Hypericum formosum††

Viola Beckwithii‡‡
Viola Sheltoni
Microsteris micrantha††
Hydrophyllum alpestre‡‡
Macronema discoideum
Dugaldia Hoopesii††
Senecio filicifolius‡‡††
Polystichum scopulinum‡‡
Selaginella Watsoni‡‡
Selaginella Underwoodii

IV. Endemic Rocky Mountain species

As the endemic element of the montane plants is very large, consisting of about 1040 species, or over 53 per cent of the whole number, it is hardly practicable to list them all. I shall therefore merely give the number of species found in each category and mention specifically only a few in each class whose distribution is particularly characteristic or of special interest.

A. Endemic plants common to the Southern and Northern Rockies

Many of the endemic plants are of wide distribution, their range extending from Colorado or northern New Mexico to Montana or even further north. To this category belong the following trees: *Pinus scopulorum*, *Populus angustifolia*, *Betula fontinalis*, and six species of *Salix* (three of these usually mere shrubs). Among the shrubs, *Sambucus melanocarpa*, *Ceanothus velutinus*, and *Svida instolonea* are the most common and most widely distributed. The category contains 6 trees, 12 shrubs, and 217 herbs, and if to these are added 7 grasses and 6 other herbs belonging to the plains and occasionally reaching the Montane Zone, the whole number of species is 248. Of these some extend outside of the Rocky Mountains, as for instance *Svida instolonea*, which reaches to Manitoba and Kansas, *Drymocallis fissa* the Black Hills, and *Scrophularia occidentalis* North Dakota and Oklohoma.

B. Plants endemic to the Southern Rockies only

1. Plants found both in the Main Range and in the Uintah-Wasatch region

To this category belong two trees, *Picea pungens* and *Populus Wislizenii*, together with 13 shrubs and 197 herbs, or in all 212 species. Of these some are limited to the very southern slope of

the Rockies and are in reality immigrants from the Upper Sonoran region, as for instance, *Populus Wislizenii*, *Grossularia leptantha*, *Blepharoneuron tricholepis*, *Calamagrostis scopulorum*, *Festuca arizonica* and *Fragaria ovalis*.

As I have stated elsewhere, the interchange of flora between the Southern Rockies and the Northern does not take place so much along the continental divide in central Wyoming as from the Wasatch Mountains, over the Bear River Mountains and the Tetons, to the Northern Rockies. Several southern species are found in the two intermediate ranges mentioned and several northern ones in the Wasatch. These southern species are as follows:

Shrub

Salix Wolfii

Herbs

Stipa Vaseyi
Rumex densiflorus
Ranunculus intertextus
Delphinium occidentale
Delphinium reticulatum
Cardamine cordifolia
Arabis divaricarpa
Potentilla filicaulis
Sidalcea neomexicana
Amarella monantha
Primula Parryi
Orthocarpus purpureo-albus
Penstemon subglaber
Penstemon Rydbergii
Aster Canbyi
Senecio perplexus
Senecio rapifolius
Senecio uintahensis
Cirsium Eatoni
Leontodon scopulorum

The following plants of the Southern Rockies extend into the Black Hills or western Nebraska.

Poa andina
Eriogonum pauciflorum
Arabis Fendleri
Draba auriformis
Saxifraga simulata
Potentilla propinqua
Opulaster monogynus
Ceanothus Fendleri
Cynomarathrum Nuttallii
Dodecatheon radicatum
Sambucus microbotrys
Thelesperma gracilis
Senecio spartioides
Senecio rapifolius

2. PLANTS FOUND IN THE MAIN RANGE BUT NOT IN THE UINTAH-WASATCH REGION

To this category belong nearly half of the endemic plants of the Southern Rockies. The list comprises 6 shrubs and 252 herbs, but no trees. Some of these are restricted to the southern slope only and may be considered as immigrants from the Upper Sonoran region. Among these are three of the four fernworts endemic to the Southern Rockies: *Cheilanthes Fendleri*, *Notholaena Fendleri*, and *Selaginella mutica*. A fourth fern, *Woodsia mexicana*, is also found in the Black Hills and in Minnesota, and ranges southward into Mexico.

3. PLANTS RESTRICTED TO THE UINTAH-WASATCH REGION

This category comprises 7 shrubs and 71 herbs, but no trees. Many of these plants are also found in the mountains of the Great Basin. Some of them, as *Fendlerella utahensis*, *Chamaebatiaria Millefolium*, *Arctostaphylos platyphylla*, *Phaca serpens*, and *Phaca Sileriana* are evidently immigrants from the Upper Sonoran region.

There are 47 local endemics found in Wyoming and southeastern Idaho which occur nowhere else in the Rockies. Of these maybe one third should be counted as belonging to the southern Rockies. If so, the total number of endemics restricted to the southern Rockies would be about 560 species.

C. PLANTS ENDEMIC TO THE NORTHERN ROCKIES ONLY

1. PLANTS OF GENERAL DISTRIBUTION WITHIN THE NORTHERN ROCKIES

Fully one-third of the endemic species of the Northern Rockies are of general distribution and extend as far south as the Yellowstone Park Region. Among these are included two trees, *Picea albertiana* and *Betula utahensis*, 4 shrubs and 102 herbs; altogether 108 species. Of these the following extend south into the Uintah-Wasatch region.

Juncus Tweedyi	*Delphinium bicolor*
Cardamine multifolia	*Aconitum divaricatum*
Ranunculus saxicola	*Draba andina*

Arabis oreophila
Arabis exilis
Micranthes Greenei
Potentilla ovina
Drymocallis foliosa
Trifolium scariosum
Angelica Roseana
Dodecatheon salinum‡
Swertia congesta
Synthyris laciniata
Orthocarpus Tolmiei
Aster amplifolius
Machaeranthera viscosa
Erigeron tenellum
Arnica arcana

The following reach the Black Hills:

Alsinopsis dawsonensis
Atelophragma glabriuscula
Atelophragma Forwoodii
Homalobus dispar
Aragallus villosus
Aragallus gracilis
Aragallus spicatus‡
Aster meritus
Cirsium Drummondii

2. SPECIES FOUND IN MONTANA AND NORTHERN IDAHO AND NORTHWARD

This category contains one tree, *Betula subcordata*, two shrubs (*Vaccinium* sp.), and 31 herbs; altogether 34 species. Of these, *Aragallus splendens* extends eastward to Minnesota, *Vaccinium membranaceum* to upper Michigan, and *V. ovalifolium* to the Gaspé Peninsula.

3. LOCAL SPECIES OR SPECIES OF VERY RESTRICTED RANGE

The local species of Wyoming and eastern Idaho number 47 (of which perhaps one third should be accredited to the Southern Rockies while 6 are also found in the Uintahs or Wasatchs), those of Montana 19, those of western Idaho 14, those of the Black Hills 5, and those of the Canadian Rockies 22 (among the latter one tree, *Betula alaskana*, and three shrubs); in all, 107 local species. If all categories of endemic species are considered, the number restricted to the Northern Rockies includes altogether about 230 species, and the number endemic to the Rocky Mountains as a whole 1,040 species.

SUMMARY

Within the Montane Zone in the Rocky Mountains are found about 1900 species. Of these, approximately 50 per cent* are

* All percentage figures in the following paragraphs are computed with reference to the total number of species.

Montane plants in the restricted sense, i. e. plants which attain their best development within this zone. Of the rest, many reach their best development in the Subalpine Zone above, and many others in the Submontane Zone below. A few alpine plants are sometimes found as low as the Montane Zone and several species from the Great Plains or from the Sonoran Zone are occasionally found as high up.

Of the plants found in the Montane Zone, 245, or less than 13 per cent, are transcontinental, i. e. they are found both in the East and on the Pacific Slope, as well as in the Rockies; 176 of these, or 9 per cent of the total flora, are common to the Northern and Southern Rockies, another 1 per cent extend as far south as Wyoming, and 1 per cent are limited to the Canadian Rockies.

Besides the transcontinental plants, there are 84 species which are common to the East and the Rockies but have not reached the Pacific Slope. If to these are added a score of western plants which have emigrated eastward as far as the Great Lakes and Hudson Bay, some of them even to the Gaspé Peninsula, Quebec, there are in all about 350 species, or nearly 18½ per cent of the flora, which are common to the East and to the Rockies. The larger portion of these, 250 species or over 13 per cent, are found in both the Northern and Southern Rockies, and 100, or more than 5 per cent, in the Northern only. None of the Montane plants are common to the East and the Southern Rockies only.

The number of species common to the Rockies and the Pacific Mountains is much larger: if the transcontinental species are excluded, about 565, or nearly 30 per cent; or, if these are included nearly 43 per cent of all the plants found within the Montane Zone of the Rockies. Nearly 450 of the plants common to the Rockies and the Pacific Mountains (the transcontinental ones included), or nearly 24 per cent of the whole number are found in both the Northern and Southern Rockies; 350, or about 18 per cent, are found in the Northern Rockies but not in the Southern, and not quite 2 per cent occur in the Southern but not in the Northern Rockies. Of the species common to the Rockies and the Pacific Mountains (the transcontinental ones not included), about 300, or nearly 16 per cent, are found both in the Cascades and the Sierra Nevada; about 225, or nearly 12 per cent, are found in the

Cascades alone, and less than 2 per cent in the Sierra Nevada alone. If the transcontinental plants are added, the percentage for the plants found in both the Sierras and the Cascades and for those found in the Cascades alone would be increased to about 20 per cent of each. The ratio for those found in the Sierras alone would remain less than 2 per cent. This refers of course to the Montane plants only. In the Submontane region the ratio would be much greater.

The endemic element consists of 1,040 Montane plants or over 53 per cent of the whole number. Of these, 245 or nearly 13 per cent are common to the Northern and Southern Rockies, 560 or nearly 29 per cent being restricted to the Southern Rockies, and 230 or 12 per cent to the Northern. Of the latter about 10 per cent extend as far south as Northern Wyoming and 1 per cent are restricted to the Canadian Rockies. Of the species restricted to the Southern Rockies over 11 per cent are common to the Main Range in Wyoming, Colorado, and New Mexico and the Uintah-Wasatch region, while 13½ per cent are restricted to the former and nearly 4 per cent to the latter. Of those restricted to the Northern Rockies, 8 per cent are found in Northern Wyoming and a little over 1 per cent are restricted to the Canadian Rockies. If the flora of the Canadian Rockies were better known this latter number probably would be much larger. We must also remember that only the region south of latitude 55° is here considered.

It may also be of interest to see how the number of species found in the Southern and Northern Rockies would compare, if all categories of Montane plants are taken in consideration. There are over 40 per cent common to both, nearly 28 per cent restricted to the Southern Rockies and 32 per cent to the Northern. The species found in the Southern but not in the Northern Rockies consist almost wholly of endemic forms, less than 2 per cent being common to the Southern Rockies (and most of these found only in Utah) and the Sierra Nevada and 3 species only being Eastern nontranscontinentals. Those found in the Northern Rockies and not in the Southern consist of over 3 per cent transcontinental species, less than 2 per cent being common to the Northern Rockies and the Eastern Canadian Zone, nearly 15 per cent common to the former and the Pacific Mountains and 12 per cent endemics: altogether 32 per cent of all Montane species.

As stated before, the interchange of species between the two great divisions of the Rockies has taken place from the northern part of the Wasatch Mountains over the Bear River Mountains and the Teton Mountains to the Northern Rockies, or vice versa, rather than along the continental divide in central Wyoming. Among the Montane plants, I have listed 69 northern species, or over 3½ per cent of the total flora, which are found in the Wasatchs but nowhere else in the Southern Rockies, and 23 Southern species, or over 1 per cent, which are found in southern Idaho or in the Teton Mountains, and nowhere else in the Northern Rockies.

A good deal could also be said about the distribution of the plants in the Black Hills, a meeting place of plants from the Northern Rockies, the Southern Rockies, the Canadian and Alleghanian Zones of the East, and of the flora of the Great Plains, and I hope to take up this subject at some future time.

NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

1917–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

OF THE

TORREY BOTANICAL CLUB

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The development and structure of the bulb in Cooperia Drummondii

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(WITH PLATES 14–16 AND NINE TEXT FIGURES)

A survey of the literature dealing with the Amaryllidaceae and closely related families reveals the lack of detailed study of bulbs, such as modern methods of microtechnique and the compound microscope make possible. The usual textbook drawings of bulbs are extremely hazy as regards the nature of the vegetative point and even of the neighboring and slightly older members. The present study is submitted with the hope of supplying a more complete knowledge of the development and structure of a typical bulb, together with diagrammatic representations of the same.

HISTORICAL

Herbert (13), in his discourse on the Amaryllidaceae, states that the genus *Cooperia* has "black shelly seeds." He received his bulbs of *Cooperia Drummondii* (12) from travelers and grew them in his greenhouse or outdoors—according to season—as he did his other plants for study. "One bulb in six months produced five successive scapes," is his experience. "As soon as the seed on one scape is ripe another seems ready to rise. . . . Its habit appears to be to flower successively from earliest spring till September with leaves principally in autumn or winter." Flowering in the greenhouse at Brown University was at its best during March and February. No successive flowering of any one plant occurred extensively. Indeed it was deemed good fortune if

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several out of a dozen bulbs containing immature flowers blossomed at all. Although no criticism is intended here on either hand, it seems fair to state that Herbert was not justified in assuming that he could determine in European greenhouses or gardens the habit of bulbs native to Texas. He found his *Cooperia Drummondii* with a "flower [which] expands always in the evening, usually not perfect after the first night." Nocturnal flowering is an anomaly, as Herbert himself states, and it seems probable that he was overzealous here in his observations, since the writer over a period of three years observed no new flowers of *Cooperia Drummondii* except in the morning and also observed no flowers opening except in the bright morning light. In fact the flowers in the greenhouse rarely shoot up as late as after eight o'clock in the morning. It is claimed that the name "rain lily" is applied to this amaryllid on its native ground, because it does shoot up into full bloom on a bright morning after a period or night of rain.

Irmisch (16–18) described in detail the structure and development of many bulbs among the Liliaceae and Amaryllidaceae, and a short article on bulbs contemporary with Irmisch's works was published by Koch (20) in 1849. In this last paper, bulbs are classified as perennial, periodic and biennial. We find in years subsequent to 1850 no important work undertaken on the bulb excepting the biological studies of Rimbach (23–28) published around 1897.

A number of articles, important indirectly if not directly, may, however, be recorded here for the future reference of other students. In 1870 Hanstein (10) published an article on embryo development in both monocotyledonous and dicotyledonous plants. The species of plants discussed in this work are of no immediate interest, yet the article deserves study and consideration because its author is a clear-headed pioneer in showing the relation of physiology to morphology and anatomy. Baillon (1) comes closer to the subject at hand while describing what seem to have been bulbiform abnormalities in the development of the embryos of *Hymenocallis*, *Crinum*, etc. The anatomy or structure of the vascular traces and secondary roots, and the relation of leaves and shoot axis in certain monocotyledons, e.g. *Allium Cepa* and *Lilium Martagon*, are well comprehended by Falkenberg (7).

The work of Solms-Laubach (30) is known and well established in reputation. Tschirch (32) describes some interesting observations in regard to the cotyledon of *Lupinus* during its development in the seedling.

Baranetsky's work (2) on the development of vegetative points in monocotyledons is exceedingly valuable, discussing as it does among other points the development of subepidermal cambium, foliar buds, ensheathing leaves, internodes and permanent tissues for nine specific monocotyledons. It enters into details of anatomy further than the present paper makes any pretense of doing. A paper on the germination of the Amaryllideae by Worsley (36), delivered before the Royal Horticultural Society, is inaccurate and needs no consideration. The structure of a garlic bulb has been described in a general fashion by Highfield (14). The duration of bulb parts, the maturity of seedling plants, and the placing of the bulb slightly below the surface of the ground by means of roots formed from the base of the cotyledon are noted briefly. Howard (15) has experimented with the mature plants of *Cooperia Drummondii*, while working on the summer rest period of plants. He does not mention any studies with "offsets."

METHODS AND MATERIAL

The mature bulbs for this study of *Cooperia Drummondii* were secured from the campus of the University of Texas through the courtesy of Dr. H. H. York, of Brown University. A portion of the bulbs planted in the greenhouse at Brown University flowered freely and produced seed, which on maturity was used to secure all young plants.

The methods of microtechnique usually followed were found unsatisfactory, since the bulbs of *Cooperia Drummondii* appear to be particularly troublesome material for embedding. Their delicate scales contain starch, a mucilaginous slime which may coagulate during killing and fixation, and crystals of calcium oxalate (see Menz, 22). The scales and stem-axis are composed of parenchyma cells and vascular bundles, which resist the sectioning individually. Material was fixed in an aqueous solution of picro-acetic* acid allowed to act for twenty-four hours. A water

* 1 gram of picric acid, 1 c.c. of acetic acid, and 100 c.c. of water.

solution of the fixing agent was found preferable to an alcoholic solution, since in fixing material such as *Amaryllis* the alcohol evidently causes a coagulation of substances present in the scales and possibly in the bulb axis. To hasten the penetration of the material by the fixing agent, the object as soon as dropped into the acid was placed in a chamber from which the air was exhausted until the large size of the bubbles arising from the cut surface of the tissue indicated a fair approach to a vacuum. The air was allowed to replace the partial vacuum very slowly without outside aid. The use of the exhaust chamber was also resorted to with every change of alcohol, alcohol and ether, and ether. The fixation was practically perfect owing to more immediate and entire penetration. It did not, however, secure even moderately good fixation of incipient roots which were wholly within the bulb axis. Prior to killing and fixation, the bulb was trimmed down to about six scales, if the purpose was merely the examination of the youngest portions. Thorough fixation was thus more easily secured and the vegetative point was not crushed by the heavier parts.

Washing was carried on in water for two days and completed in the low grades of alcohol, such as 20–70 per cent. The general celloidin method was followed from here on until the actual point for embedding was reached. At this point in the work, the object, after the removal of the superfluous celloidin, was hardened in 70 per cent alcohol and then in chloroform for two hours. It was transferred from the chloroform to 85 per cent alcohol. The usual paraffin method of imbedding was now followed (5). Material prepared in this way sectioned with unusual smoothness and ease.

The rotary microtome was used in all paraffin work except where bulbs or pieces of material were too large for the section block. Such large pieces of material were mounted on blocks of wood, trimmed out underneath until small enough to be placed in the jaws of the sliding microtome clamp. In handling individual paraffin sections as large as, or larger than, two inches square, a vessel of warm water was kept at hand. The sections placed carefully on the surface of the warm water uncurled readily, with no danger of cracking. It is necessary to see that the water is not

too warm at first. A few changes of the water to warmer or reheating of the water by placing the container in another vessel of warmer water will be found useful.

MATURE EMBRYO

The structure of the mature embryo as seen in relief exhibits a scarcely protruding pocket, which protects the leaf-primordium and the vegetative point by surrounding their outer surface as they lie against the base of the cotyledon. The sheath-like base of the cotyledon has no vascular system and is very simple in structure. The long spindle-shaped cotyledon is succulent and projects into the mass of endosperm, absorbing food for the developing embryo by means of a layer of thin-walled parencyhmatous cells running parallel with the longitudinal axis of the embryo. The suspensor, which is composed of either one or two cells, still holds the embryo in position at maturity.

The number and size of the leaf-primordia, developed at the time the seed is ripe, are not at all constant but depend on the individual embryo. No cases have been noted, however, where the first leaf-primordium had not made its appearance at this period. The primary root is protected by a well-developed root cap even as early as the maturity of the seed.

Wordsell (35) has recently given to botany a comprehensive paper on the monocotyledonous embryo, where extensive discussions and a bibliography relating to the cotyledon may be found. His opinion is exactly that of Čelakovsky, namely, that the cotyledon is an equivalent of the capsule of the moss sporogonium, just as the hypocotyl is of the seta. Goebel (8) states in regard to the cotyledon of the seed plants: "I need only say here that the cotyledons, which so frequently differ in form from the foliage leaves, are merely arrested forms of these, the arrest being sometimes permanent, sometimes transient." Lyon also has contributed (21) to discussions of the true morphological position of the cotyledon. At best a discussion becomes one of terminology unless combined with detailed anatomical observations on serial sections of embryos at successive ages of development. The present writer is inclined to agree with Lyon, stating that as the cotyledon of *Cooperia Drummondii* does not appear to arise as an

exogenous lateral outgrowth upon the growing point of a stem as do the later foliar structures, therefore, said cotyledon, occurring in the mature seed plant at the base of the primary stem, is more closely related to the nursing foot of the bryophytes. The succulent cotyledon of the young plant of *Cooperia Drummondii* in anatomical structure and size is well adapted to serve as an absorption organ.

SPROUTING OF THE SEED

The ripe seed of *Cooperia Drummondii* was described by Herbert (13) as having a brittle, shiny black seed coat and inclined to be wedge-like in shape. The seed coats are slightly torn at the time of sprouting as the root pushes through the very small micropyle, but they are never split apart into halves. On February 20, 1914, the seeds from a ripe pod were immediately placed upon wet filter paper on the sides of a moist chamber at ordinary room temperature. Three days later—February 23—the seeds had sprouted and the roots on the seedlings averaged 4 mm. in length; on February 25 the root length was 10–12 mm., while at thirty days of age the root length was 65 mm. If, however, the seeds were well dried and allowed to remain dry for several months at the temperature of the laboratory they did not sprout so readily.

The future root and shoot of the embryo are pushed out of the seed coats by a lengthening of the cotyledon, as well as by the growth of the root- and shoot-regions. Solms-Laubach (30) notes a similar condition in *Heterachtia*.

The portion of the cotyledon between the micropyle region of the seed coats and the surface of the soil becomes a brilliant green, indicating the formation and presence of chlorophyll here. The cotyledon therefore functions in part as a leaf, aiding the leaf blades in the photosynthetic processes of the plant's activities. The leaf grows upward to the light above the ground, while the cotyledonary sheath serves as a protecting sheath in the same fashion as the encircling leaf base of any subsequent leaf serves as a sheath for the next younger leaf (FIG. 4). The region bounded by the root, the cotyledon and the plumule was designated by Richard (29) in 1808 as the "tigelle," corresponding as he said to the Latin term "cauliculus." The "tigelle" he defines as

merely a "prolongement" of the "radicule," explaining that "la Tigelle (Cauliculus) se confond d'une part avec la Radicule dont elle n'est qu'un prolongement et se termine de l'autre à la base de la cavité cotylédonaire." Jussieu (19) agrees with Richard and also connects the "tigelle" up with the term "carnode" of Cassini and with Brongiart's "mealy body" found in *Lemna*, although the describer says the latter even may be a cotyledon. At this region designated as the "tigelle" the writer noticed in *Cooperia Drummondii* that the cells divide in planes at variance with the tissues of the shoot above it and the root below it (FIG. 10, *h*). Here they divide in both the horizontal and tangential planes with little lengthening and practically no broadening, while in the shoot and root the cells broaden relatively rapidly and also elongate greatly.

The area enclosing the axis of the first leaves and the growing point (the plumule, the "gemmule" of early writers) is potentially cotyledonary. Lyon (21) states that the maximum development in this area takes place at the point or points that are in the most favorable position to function, and that in monocotyledons the maximum development occurs only on one side. And, further, that cotyledons *do not* arise as exogenous lateral outgrowths upon the growing point of a stem as do all later foliar structures. The gross anatomy of *Cooperia Drummondii* indicates that there is a point of maximum development and also one of decidedly minimum development in the cotyledonary region. Also the anatomy of the developing embryo shows us that the cotyledon does not develop from the vegetative point, nor does the cotyledonary sheath. The function of each of these portions is peculiar to itself, the maximum point of development elongating into a haustorial organ with the function of absorbing food for the germinating embryo, the point of minimum development not elongating but serving as a protective covering or a sheath to the primordia or a pocket in which the gemmule is deposited, according to the older writers, as a ball is in a cup. The gemmule is thus defined by Richard (29): "La Gemmule (Gemmula) est la petit corps simple ou composé qui nait ou du fond de la cavité cotylédonaire, qui le referme étroitment." The early scientists noticed that their "gemmule"—the vegetative point plus an

incipient leaf or so—could be sighted through the "fente." As Jussieu (19) states: ". . . et ce ne fut qu'apres des recherches répétées et minutieuses que je parvins à m'assurer que le cotyledon présentait en effect une petite fente vers sa base." They speculated as to whether or not this gemmule were naturally detachable from the rest of the structure. Brown (3) speculates in his work and merely shoulders enough responsibility to say that the gemmule in bulbiform amaryllids can be seen and that it escapes through this opening, "petite fente."

A careful microscopic examination of slides of a five-day-old *Cooperia Drummondii* seedling reveals cell structure indicating that root contraction has already begun. Such a condition has been noted by Hällström-Helsinke (9) in *Urginea maritima*, by Rimbach (23-28) and by De Vries (34) among the dicotyledons and also in *Hyacinthus orientalis*. Rimbach appears to be the best-known investigator volunteering a hypothesis of the relation of this contraction to root tissues. It is the intention of the writer to discuss his deductions and those of others later.

THE SEEDLING

A five-day-old plant of *Cooperia Drummondii* (FIG. 1) shows no outward indication of bulb formation. However, the region *h* does limit the territory of the root and of the shoot. The primary root is a tap root, in appearance stout, tapering slightly downward, and colorless. The shoot consists of the first leaf blade or lamina, l_1; the cotyledon, *c* (from which in the preparation drawn portions of the seed coats and of the endosperm tissue, *e*, had been removed); and the cotyledonary sheath. A central longitudinal section of this individual (FIG. 2), under the low power of the microscope, shows in addition the sheath, b_1, of the first leaf and the primordia of the second leaf, l_2 and b_2, together with the vegetative point, *pm*. The stippled strips represent approximately the space occupied by the vascular traces, no branch of which goes to the cotyledonary sheath, *cs*. FIG. 3 takes to one side the youngest area and represents exactly its cellular structure. In this region, surrounded by the first leaf of the young plant, the cells are actively dividing. The cells at l_2 and b_2 indicate not only that the second leaf has already become differentiated from the primordial meristem, *pm*,

but also that as a whole the meristematic tissue of this second leaf occupies an area placed diagonally to the longitudinal axis and surrounding the primordial meristem like a collar. The primordial meristem is often definitely composed of paired cells (FIGS. 3 and 6, *pm*), as Carano (4) has recorded for *Yucca*. Each new leaf arises from a group of subepidermal cells (Barenetskey, 2), which become meristematic and divide tangentially. Thus a new tissue is formed which, as it pushes out, becomes a future leaf. As the first leaf is thrust out far from the cotyledonary sheath into the air (FIG. 4), the cotyledon elongates and curves downward until it is parallel with itself and the vertical shoot, thus passing through an angle of 180 degrees (FIG. 4).

THE TWO-MONTH-OLD PLANT

When the food supply has been exhausted or drawn upon to the necessary extent the cotyledon, having no further need to serve as a haustorial organ, becomes shriveled up and dies (FIGS. 5, and 14). With this dying off of the cotyledon the dry, hard seed coats with any residue of endosperm drop to the ground or at least cease active relations with the cotyledon.

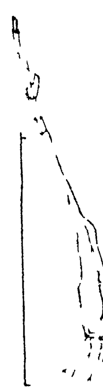

FIG. 1. One-year-old bulb; scale = 5 cm.

The second leaf bladé usually reaches daylight between the fifty-fourth and the sixty-first day (FIG. 14). As the first leaf sheath is surrounded by the basal sheath of the cotyledon, so this second leaf sheath is surrounded by the basal sheath of the first leaf, in respect to which it is distichously placed. In *Tulipa* the leaf lamina, as is well known, does not always develop. Henry (11) makes note of this fact in his discourse, "Beiträge zur Kenntniss der Laubknospen." Even in young bulbs of *Tulipa* the aborted scale-like leaf alternates with a true leaf bearing a green lamina. In *Cooperia Drummondii*, however, the lamina always develops and as a result we have in this member of the *Amaryllis* family no mere sheath- or scale-leaves. The lamina of the leaf of *Cooperia Drummondii* appears to develop simultaneously with its respective base. The incipient bulb is now readily recognizable (FIGS. 5 and 14). Its outer and only scale is formed

of the cotyledonary sheath. The bulge shown (FIG. 14) is due to a young root. This first adventitious root, *r*, originates (FIG. 8) at the node of the second foliar leaf and, growing downward, cuts its way through the first leaf and the cotylar sheath. A slightly older root with a well differentiated root cap and primary tissues (dermatogen, periblem, and pleurome) is shown in FIG. 18. This seedling is from the same planting as that of FIG. 8. The young root arising endogenously in the bulb- or stem-axis will, together with similar companions, replace the tap or primary root. The primary root is still active at this time. The secondary roots, which become functionally the principal roots of *Cooperia Drummondii*, are adventitious roots, derived from an active cambium tissue below and to one side of the growing point. They force their way through the tissue of the bulb-axis and form at first roots to one side of the early dying primary root and later a complete ring of such roots. The roots of *Cooperia Drummondii* have root hairs. The vascular bundles which develop in the secondary roots anastomose with the bundles already formed in the stem-axis. The complete working out of the origin and arrangement of the vascular traces in the stem-axis of *Cooperia Drummondii* would be very difficult, so complicated is the anastomosis. Both the primary root and the secondary roots show a wrinkling on their surface which is connected with the drawing down of the bulb into the soil by contraction of said roots. A bulb may be drawn down in this fashion to a depth of over seven inches.

The puckered or wrinkled condition of the primary roots (FIGS. 8, 15, 17 and 18) is due to contraction of at least some of the tissues. This phenomenon occurs in the adventitious roots also. Its hypothetical mechanics will be discussed later. The outlay of root tissue in FIG. 17 has a narrow slice marked off. This slice has been divided into three sections—1, 2 and 3. If this narrow strip of root is studied with the high power of the microscope we have under observation cellular tissues similar to those of FIG. 19, where 1 represents the vascular region; 2, the parenchyma; and 3, the cork and other dead tissues. Evidently the root contraction has entirely damaged only the outer cells, which are now dead tissue. The inner cells have in some way accommodated themselves in part to the strain. The trace is still intact although

its individual cells are irregular in diameter, presumably from the effects of some pressure. The parenchyma cells outside the trace are still equipped with cytoplasm and nuclei, although some force has pushed them by each other and flattened their nuclei.

ROOT CONTRACTION

The first reference in the literature to root contraction, according to De Vries (34), is that of Tittmann (31) in Flora for 1819. Under "Wurzelbildung" Tittmann describes the contraction of the roots in *Daucus Carota* as follows: "Der Stengel wird dicker und kürzer, zieht sich gleichsam in die Erde hinein, oder wird von derselben angezogen, und man findet dann nach einiger Zeit die langen Saamenblätter dicht auf der Erde ausgebreitet. Untersucht man in dieser Periode die Wurzel, so hat sich die Gränze zwischen ihr und dem Stengel, der sich nun auch in der Erde befindet, ganz verloren und ausgeglichen."

De Vries (34) himself worked principally with dicotyledons, experimenting with eighteen species of plants. He studied the effects of exposure to air, to water and to salt solutions on strips, separate pieces of definite tissues, and single cells of roots. He measured changes in length, width, and volume of tissues and cells. He considered roots from plants still bearing succulent cotyledons to those two years of age. He studied young roots and roots two years old. Each experiment is considered in itself and in the light of previous experiments, until at last he concludes that root contraction is not due to intake of water but to changes in turgor and remarks that the thoughtful reader will ask, "durch welche Ursachen die ungleiche Dehnbarkeit der Zellhäute selbst bedingt wird."

Rimbach discusses root contraction as it occurs in *Colchicum autumnale* (26), *Arum maculatum* (28), and *Allium ursinum* (27). He found that, in the case of naturally deep-set bulbs of *Allium ursinum*, a depth of 10–15 cm. was attained after several years by the contraction of the roots. In explanation as to how contraction in roots comes about he states, that, while the root tip holds firmly to the earth particles, the endodermal cells contract longitudinally as a result of a tendency to lengthen radially and tangentially, which results in the contraction of the root. The bulb yields to

this pull, which results from the contraction of the roots, and is gradually placed more deeply in the ground with each new set of roots. Even the upward development of the shoot, where the lowest and oldest scales are each formed at a slightly higher level, does not counteract entirely this forced downward movement of the bulb. Therefore the bulb is continually placed more deeply in the soil.

In *Arum maculatum* Rimbach (28) explains that the active portion of the root consists of the cells directly below the epidermis and the "hypodermal layers." These cells shorten in their length as much as one half and their radial walls lengthen somewhat. The vascular bundles and their accompanying cells are not active. However, the latter respond sufficiently to the vertical pressure caused by the shortening of the parenchymatous cells just outside them to show definite wrinklings along their walls, and the tracheal tubes themselves shorten between the rings.

Rimbach's careful observations and well-chosen biological experiments are not supported by his theoretical conclusions. Because he has accurately noted that endodermal cells lengthen radially, he proceeds to state that they shorten longitudinally and that therefore the whole root contracts, with the result that the bulb is set more deeply into the ground. All other tissues are passive, yet they must be shortened in the shortening of the whole root. Without sufficient morphological proof Rimbach claims that the outer or cork cells are crushed and killed, and that the vascular cells are thickened. The outer cells are crushed doubtless, but do they die first or are they killed by the crushing? His further conclusion that the vascular cells thicken may be true, but where is his proof? To return to the active or endodermal cells, how can we accept the statement that because a cell lengthens in one direction therefore it must necessarily shorten in another? Volume being constant and cell wall composition and tension being similar at every point this would be true; but Rimbach did not investigate these points.

Rimbach states that ripples may be seen on the root surface even to the root-ends with the naked eye. Microscopic slides have proved to the writer that the process of root contraction is well under way in a five-day-old seedling of *Cooperia Drummondii*

at points not visible to the naked eye. The ripples in individual cells are not confined to radially placed cell walls, as Rimbach finds them to be in the species which he investigated. On the contrary they may be found on walls running in any direction. In some stages they are so fine as to be distinguishable only with the oil immersion objective, but always numerous cells with rippled walls may with care be detected in the parenchyma cells of the root with a combination of 10 ocular and 8 objective.

The warped and altogether disorganized condition of the epidermis and "hypodermal" layers in the contracted roots of *Cooperia Drummondii* may be comprehended, if we study the tissues represented by the blackened areas in FIG. 17, section 1.

It seems safe to accept these facts: (1) roots do shorten; (2) the parenchymatous tissues of the root are the seat of this activity; (3) the cork and the vascular trace are passive; (4) the cork is ultimately crushed; (5) there is a region where one can see wrinklings and measure shortening, a second region where no wrinklings are visible yet where one can measure shortening, and an unchanged region (Rimbach); (6) in dicotyledons the trace becomes visibly curved inward and outward in a wavy fashion, while in monocotyledons the vascular bundles remain practically straight (De Vries).

What remains to be determined constitutes a problem of botanical research as yet unsolved. We may hope that some worker with an interest in morphology as well as physiology may master this problem by a study of serial sections of young roots and a consideration of the physical relation of turgor and biochemical alterations in the protoplast and cell membrane.

All the roots of a plant may not shorten equally. *Phaedranassa chloracea*, according to Rimbach (**25**), has a main root which shows no shortening. In other cases none of the roots shorten. *Tulipa*, according to Döring (**6**), is a case in point. The bulb here would not be pulled down since its roots spread out almost parallel with the surface of the soil.

THE SCALES

The scales, that is, the leaf sheaths, which constitute the greater portion of the bulb, are differentiated into certain tissues, represented diagrammatically in FIG. 7. A scale has an epidermal

layer on each surface. The several rows of cells directly below the outer epidermis contain starch, while the cells below the inner epidermis do not. The starch-filled cells measure 59–158 μ in length and 59–69 μ in width, with their greatest dimension running parallel to the longitudinal axis of the bulb. The vast majority of such cells average 158 x 59 μ. The cells between the cells containing starch and the accompanying cells contain raphides in the first seven or so scales, but rarely in the older scales. The amount of starch also is less in the older scales than in the more actively functioning portions of the bulb. There appear to be, however, sphaero-crystals stored in the older scales. There is noticeably less starch and fewer raphides in the scales immediately

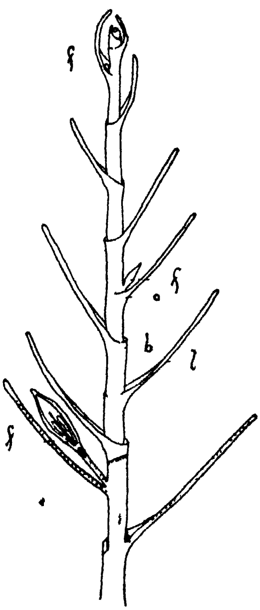

FIG. 2

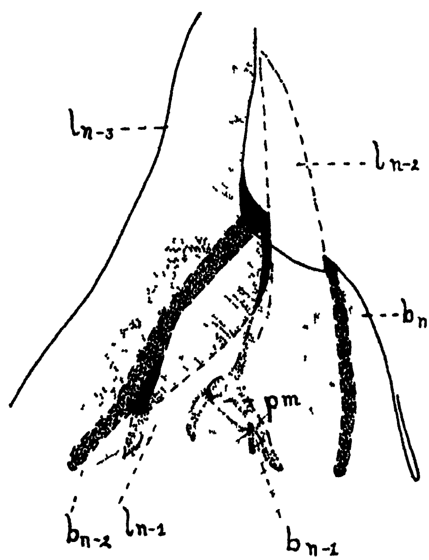

FIG. 3

FIG. 2. Diagram of *Cooperia Drummondii* as it would appear if the internodes developed. *l*, lamina of a leaf; *b*, basal sheath; *o*, leaf subtending flower; *f*, flower; in the lower part of the figure a central longitudinal section is represented, showing principally the relation of the basal sheath to the main axis; the relation of the flower and its subtending leaf to the main axis is problematic with the evidence at hand.

FIG. 3. Diagrammatic semi-transparency of the youngest portion of the bulb of *Cooperia Drummondii*. *pm*, the primordial area, below which are the primordia of the youngest or *n*th leaf; successively older leaves are marked l_{n-1}, l_{n-2}, and l_{n-3}; their respective bases, b_{n-1}, b_{n-2} and b_{n-3}.

following the flower stalk which has most recently died, and finally neither starch nor raphides are to be noticed in the outermost and oldest scales. The leaf bases in the youngest portion of the bulb—the only portion within the bulb itself where the leaf base in cross section is scarcely continuous with the lamina—have no starch stored in them. The leaf accompanying the flower is supplied with starch even when it is very young. Young roots that have not yet pierced the bulb-axis contain raphides. The starch grains and raphides, therefore, are most prevalent in the younger scales. Here cells with raphides may be found among the tissues containing starch or scattered between the starch-bearing cells and the accompanying cells, but most commonly they are found in rows of cells. An individual cell in such a row is about twice as long as a starch-bearing cell or often still longer. The sheath or bundle of crystals practically fills the cell containing it. Measurements of the raphide-bearing cells show that their dimensions measure 277–475 μ in length and 79–99 μ in breadth. The remainder of a scale is composed of vascular bundles and their accompanying parenchyma, the cells of which are intermediate in length between the cells filled with starch and those with raphides. The dimensions of these rather simple cells range from 178 x 119 μ to 297 x 69 μ.

Miss Menz (21) has made observations similar to the above in connection with *Amaryllis*, *Zephyranthes*, *Sternbergia*, *Crinum* and *Allium*, finding in the scales of these genera starch, raphides of calcium oxalate and also a latex-like or slimy substance stored as reserve material.

DEFINITION OF A BULB

Bulbs, according to Irmisch (16), have been looked upon as roots, underground shoots, and downward growing shoots, while Irmisch himself concludes with the emphatic statement that a bulb is a bulb—an organ peculiar to certain plants and distinctive in itself.

A bulb is a shoot in which the internodes have not developed or have developed only to a small extent (TEXT FIGS. 1, 4 and 5). The peripheral layers of the bulb consist of the bases of the foliar sheaths. As there are no internodes in the shoot of *Cooperia Drummondii* its foliar sheaths never can form an exterior covering

to internodes but instead surround the next younger sheath, as they themselves are surrounded by an older sheath.

If a shoot, developed as is usual in herbaceous plants, corresponds to a telescope drawn out for observation of the stars, a bulb finds its correspondential in the same telescope pushed in—i.e. a bulb is a foreshortened or a "telescoped" shoot (TEXT FIG. 2). A bulb of *Cooperia Drummondii* is probably never raised above the earth's surface. It is constantly being set deeper into the ground. The oldest tissue composing the base of the truncate bulb axis is continually sloughing off, while the youngest tissue is continually formed at a point farther and farther away from the point where the primary root originated. This setting of the bulb deeply into the ground is due to root contraction, which has been explained as far as is possible with our present knowledge before us. An old bulb of *Cooperia Drummondii* may ultimately bear a neck 15–18 cm. in length.

"OFFSETS"

The "offsets" or "splits" arise between the mature scales as protrusions. When conditions fostering vegetative propagation occur, the "splits" develop (FIGS. 12 and 13; TEXT FIGS. 4 and 5) between the scales or leaf sheaths and break their way through the outer and older bulb scales, in an effort to reach the soil. They develop on alternate sides of the axis and frequently occur between every five scales. However, there seems to be considerable variation in regard to this matter of arrangement.

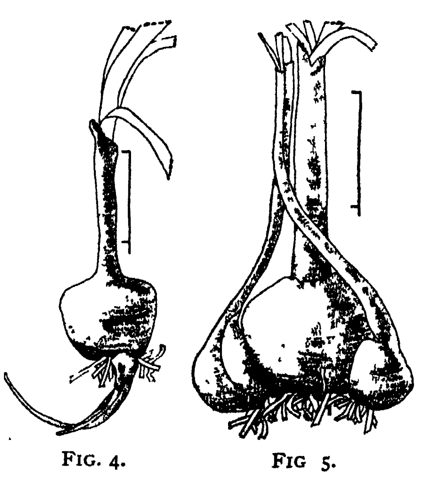

FIG. 4. FIG 5.

FIG. 4. "Offset" readjusting itself after an unfavorable start; roots diagrammatic, i. e. wrinklings due to contraction omitted; scale = 5 cm.

FIG. 5. Vegetative propagation displacing flowering; roots and leaves diagrammatic; scale = 5 cm.

Henry (11) notes that *Gagea arvensis*, *G. stenopetala* and

Tulipa sylvestris show secondary bulb formation from the original bulb developed to extreme abnormality, yet every bulb so formed is always a leafy shoot. That is, such a bulb is a secondary or lateral shoot, or a terminal shoot which will eventually separate itself from the growth of previous years. Vigier (33) relates a few casual but interesting experiments with bulbil formation in cuttings of *Lillium candidum*. Bulbils did not form on the cuttings, unless the end of the cutting and thus the terminal bud were injured accidentally or intentionally. Nipping the terminal bud of horticultural plants to produce lateral branching is a common horticultural practice. Regarded as lateral branches these bulbils are unique only in their being vegetative outgrowths which can of themselves reproduce the plant vegetatively, where the usual secondary branch can not do so without the gardener's aid. The bulbils of *L. candidum*, formed in the light above ground, were in Vigier's experiments green with purple spots, while those formed on the part of the cutting under the soil were white. There can be no proof brought up against the statement that there is primarily no difference between these bulbils of *L. candidum* formed below or above the ground and the offsets, splits, or brood-bulbs of *Cooperia Drummondii*, for instance. There is no difference even between the bulbils formed in Vigier's experiments: whether the said bulbils have green and purple pigment or are colorless; whether they are formed above or below the surface of the ground; or whether we are considering a bulbil or what is recognized commonly as a lateral shoot. In each case we have a shoot—a structure which is still a shoot none the less, whether it be a main or lateral shoot, or an artifically aborted shoot, or (as is the bulb) a naturally aborted shoot, in which the internodes have elongated little if at all.

THE MATURE BULB

Irmisch (16, 17) describes the structure of immature and mature bulbs of *Amaryllis formosissima* (now *Sprekelia formosissima*). His work presents to us a most careful research, recorded by the observer's skilfully executed drawings. While further investigation since 1850–60 causes us to feel certain in regard to points which are here discussed rather lengthily and

left undecided even then, and to disagree with some conclusions which Irmisch does draw, yet the ground is covered so minutely and the observations are presented so carefully that the work is worthy of our close consideration. According to Irmisch *Amaryllis formosissima* has in the mature bulb, considered first of all from the outside toward the inside, three or four leaves with

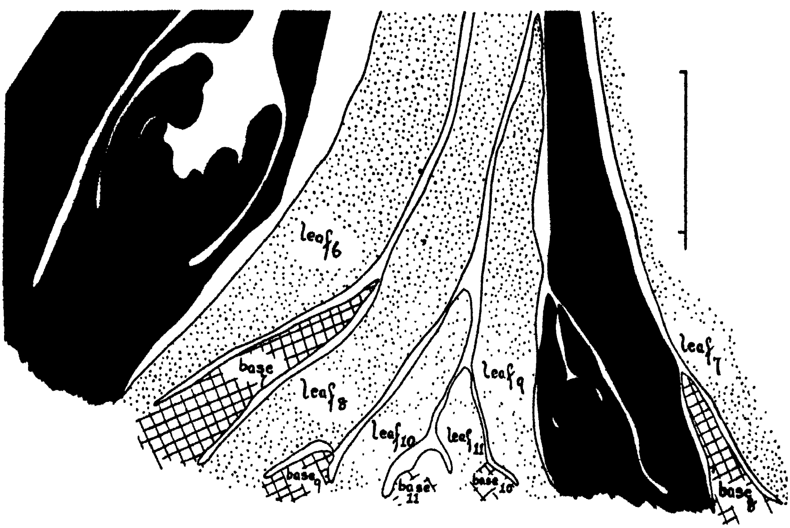

FIG. 6. Central longitudinal section of youngest portion of mature bulb; camera-lucida drawing of portion cut off between dotted lines at center of PLATE 16, FIG 17: black areas represent the flower and its subtending leaf; stippled areas indicate the portions of the leaves which becomes laminae; cross-hatched areas show the leaf bases; plain areas are primordial tissue; it is presumed that the oldest leaf shown is the sixth leaf—an arbitrary choice. Scale = 0.1 mm.

closed bases. Such a leaf he terms "Schale," which literally translated into English means "skin" or "hull" and again has the derived meaning, "bowl." This seems a most apt scientific term, for one can readily understand that if the center of a bulb is removed, leaving only a few outer scales there is left merely a few skins, bowl-like in shape. Following the three or four leaves with closed bases, there is one leaf with an open base which subtends a flower scape. Such a leaf is termed by Irmisch "Schuppe," which means "scale" (as of a fish) or "shovel" in English. Apart from the blade the open based leaf accompanying the flower of *Cooperia Drummondii* is shaped decidedly like a scale and with

the blade attached becomes the shovel. In the case of *Amaryllis formosissima* there is in the axis of this open based leaf an axillary shoot or secondary branch whose terminal bud becomes a flower. This flowering scape has two leaves which are not normally developed. The flowering branch is followed by three or four leaves with closed bases similar to the first group, but always growing smaller and more rudimentary as the primordia are approached. An old bulb might have within it four flowers with their accompanying "Schuppen" and thirteen to fifteen scales. Usually all laminae are dead at flowering times, Irmisch states, and the new leaves come always from that portion of the bulb inside of the last flower. The occasional open leaf does not alternate with the closed leaves, so that diagrammatically Irmisch's interpretation might be represented as in TEXT FIG. 7, *a*. In *Galanthus* and *Leucojum*, however, Irmisch does find alternation between Schuppe and Schale (TEXT FIG. 7, *b*). The present writer has observed for *Cooperia Drummondii* the same relation of the two types of leaves as Irmisch did for *Amaryllis formosissima*, which again relates *Cooperia* closely to *Amaryllis*. In *Cooperia Drummondii*, however, the axillary bud develops only one bract besides the flower from its terminal primordium. This is represented diagrammatically by TEXT FIGS. 2 and 9.

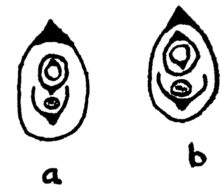

FIG. 7. Cross-section diagrams after Irmisch: *a*, of *Amaryllis formosissima*; *b*, of *Galanthus* or *Leucojum*; in *Galanthus* and *Leucojum* Irmisch found alternation between "Schuppe" and "Schale"; in *Cooperia Drummondii* and *Amaryllis formosissima* the open-based leaf subtending the flower does not alternate with the closed leaves.

The shovel-like leaf accompanying the flower is open at the base in *Cooperia Drummondii* whether the flower matures or not, but in *Narcissus* and *Leucojum* the base of the same type of leaf becomes closed if the flower never develops. In *Cooperia Drummondii* this leaf may belong to the lateral axis which gives rise to the spathe-like bract and the flower. *Cooperia Drummondii* has no stipules unless the base opposite the lamina was once formed by the fusion of such (TEXT FIG. 8). It seems, however, as if the base were here derived from a slight and all-encircling outgrowth of the primordial meristem of each individual leaf primordium.

The mature plant of *Cooperia Drummondii* has a subglobose bulb, increasing in size with age. The outermost scales have become thin, dry, brown membranes, whose venation is readily seen. As one goes inward, tearing away the scales, those with dried edges are succeeded by fresher and thicker scales. Every third scale is separated from the next younger or older scale, according as we work inward or outward, by a scale accompanying a flower peduncle, and this arrangement is repeated in accord with the age of the plant, the parts always growing smaller and more rudimentary. An old bulb may contain the vascular traces and dried stalks of numerous past or undeveloped flowers, and immature flowers for three successive flowerings (see TEXT FIG. 9).

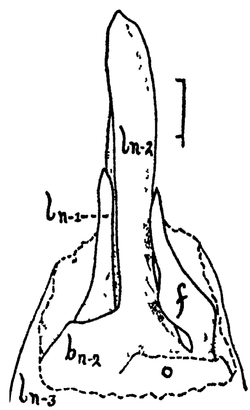

FIG. 8. Central portion of bulb showing immature flower; presuming there are n leaves, the first left we see is the $n-1$ leaf, which is surrounded by the $n-2$ leaf with its base and lamina designated as b_{n-2} and l_{n-2} respectively. This is in accordance with FIG. 3; f, an immature flower, and o, its subtending leaf with an open base. Scale = 0.15 mm.

Irmisch (16) gives a type classification of bulbs supplemented with examples, Latin designations and a set of symbols. The first type is designated as "*Gagea*-Arten," and the symbol expression corresponding is G+Z, where G is equivalent to "Gegenwart" and Z equals "Zukommen," next year's development. Therefore all bulbs similar to *Gagea* consist of G (present, active portions) and Z (tissues capable of repeating the life story next year). Another type, e.g. *Galanthus nivalis*, is represented by the symbols 1V+G+Z. 1V is equivalent to parts of the preceding year which are now present as "Nahrblätter" or sheaths containing stored material. Yet another type, *Amaryllis formosissima*, may be represented by 2V + G + Z, where the parts of two previous years still remain. *Cooperia Drummondii* might be represented by nV + G + Z where n varies largely with environment as well as with the age of the plant.

The following scheme, illustrating a mature bulb of *Cooperia Drummondii*, may likewise be considered in connection with TEXT FIGS. 2, 6, 8 and 9:

MAIN AXIS OF BULB

Three leaves with closed bases (Schalen).
Lateral axis:
 One leaf with open base (Schuppe), position problematic;
 One bract subtending flower;
 One flower (terminating lateral axis).
Three leaves with closed bases.
Etc. to vegetative point.

Galanthus and *Leucojum* also have open-base leaves succeeded by a flower stalk, but their open-base leaves alternate with the closed-base leaves. The open leaves do not alternate with the

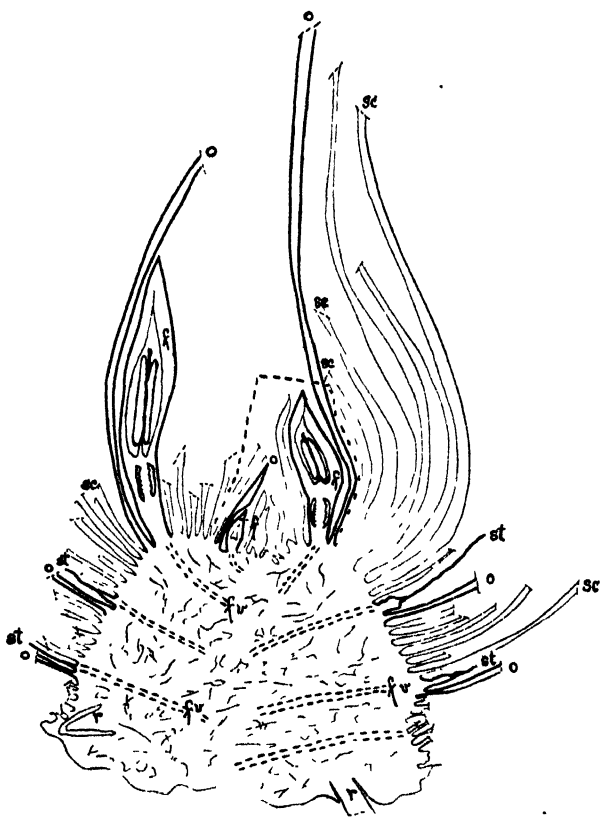

FIG. 9. Diagrammatic longitudinal section of mature bulb showing the main axis drawn in thin lines; the flowering axis (?) in heavier lines; the section between the dotted lines may be seen enlarged in TEXT FIG. 6.

closed-base leaves in either *Amaryllis formosissima* or *Cooperia Drummondii*, but with each other (TEXT FIG. 7, *a* and *b*). The

flower peduncle, terminal in respect to the lateral axis, is subtended by a spathe-like bract.

CONCLUSIONS

1. The mature seed of *Cooperia Drummondii* germinates with little difficulty.

2. A five-day-old seedling shows a tap root, hypocotyl, and one young leaf blade.

3. A ten-day-old seedling exteriorly shows no indication of bulb formation.

4. Seedlings by their fortieth to fiftieth day of growth have developed a typical bulb formed from the closed bases of alternate leaves.

5. The bulb is set deep into the ground by a contraction of the roots, which begins as early as the fifth day.

6. A mature bulb is composed of a thickened axis (with morphologically aborted internodes), from which develop (in a downward direction) adventitious roots, piercing the outer edge of the axis in a circle, and (in an upward direction) scales (leaf bases), flower scapes (each with its accompanying open base leaf), and leaves.

7. The flower scape and the leaf accompanying it alternate with the next younger corresponding leaf and scale; they arise between every third and fourth scale.

8. Vegetative buds of a type called "offsets" among horticulturists develop between the scales whenever conditions of environment are unfavorable to flowering.

9. A bulb is a foreshortened vegetative shoot which appears aborted, because the internodes do not develop, while the nodes are thickened by irregular and considerable multiplication of cells.

This paper was presented in 1918, in partial fulfillment of the requirements for the degree of Doctor of Philosophy at Brown University. The writer begs to acknowledge the assistance given by Professor Harlan H. York of the Botanical Department.

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Explanation of plates 14-16

The following remarks refer also to the text figures. FIGS. 7, 12 and 13 in the plates and TEXT FIGS. 1, 4, 5 and 9 are not camera lucida drawings. All other drawings except the diagrams are camera lucida drawings from actual living plants or microtome sections of the identical plants Except for FIG. 10, where a Bausch and Lomb camera lucida was used, the Zeiss camera lucida was employed. A Leitz-Wetzler compound microscope was used as a rule. FIG. 10, however, was made with a Zeiss microscope. The longitudinal sections were cut in a plane at right angles to the broad surface of the lamina of the leaf. The scale of magnification is indicated for most of the figures. The following symbols are employed: *b*, leaf base; *c*, cotyledon; *cs*, cotyledonary sheath; *e*, endosperm; *f*, flower stalk; *fv*, flower trace; *h*, bulb-axis or "tigelle"; *l*, lamina; *o*, open-base leaf; *pc*, procambium; *pcs*, procambial strand; *pm*, primordium of stem; *r*, root; *sc*, closed leaf; *st*, old flower stalk; *t*, testa.

PLATE 14

FIG. 1. Five-day-old seedling; one half of the seed coats and the endosperm has been removed to show the cotyledon; *h* is the hypocotyl, and *l*, the first leaf; see FIGS. 2 and 11; scale = 1 cm.

FIG. 2. Central longitudinal section of five-day-old seedling, showing the sheath, b_1, of the first leaf, l_1, and the primordia of the second leaf, l_2 and b_2, together with the vegetative point, *pm*; the stippled areas show the location of vascular traces; scale = 0.1 mm.

FIG. 3. Vegetative point of five-day-old seedling (see FIGS. 1 and 2 for comparison); in this region surrounded by the first leaf of the young plant cells are actively dividing; the cells at l_2 and b_2 indicate not only that the second leaf has become differentiated from the primordial meristem, *pm*, but also that as a whole the meristematic tissue of this second leaf occupies an area placed diagonally to the longitudinal axis and surrounding the primordial meristem like a collar; scale = 0.1 mm.

FIG. 4. Ten-day-old seedling; as the first leat is thrust out far from the cotyledonary sheath into the air the cotyledon elongates and curves downward until it is parallel with itself and the vertical shoot, having passed through an angle of 180 degrees; scale = 1 cm.

FIG. 5. Thirty-seven-day-old seedling; b_1 is the base of the first leaf, l_1, and l_2 is the second leaf; scale = 1 cm.

FIG. 6. Primordia of the thirty-seven-day-old seedling; scale = 0.1 mm.; l_4 and b_4 should be transposed.

FIG. 7. Diagram showing relative proportions of epidermal cells, raphide-bearing cells, starch-bearing cells and vascular traces; scale = 0.22 mm.

PLATE 15

FIG. 8. Longitudinal section (not quite through center) of thirty-seven-day-old bulb; note young root cutting way through base of the first leaf; this root arises at the third node and at the base of the second leaf; scale = 0.1 mm.

FIG. 9. Primordia of the fifty-four- to sixty-day-old seedling shown in FIG. 14; not a central section; scale = 0.1 mm.

FIG. 10. Longitudinal section (not central) through slightly developed plant to show region, *h*, dividing shoot and root in its early formation; l_1 is the first leaf.

FIG. 11. Primordia of bulb shown in FIG. 15.

FIG. 12. Detached young "offset" with two scales already formed; it arises from between the mature scales as a protrusion.

FIG. 13. Young "offset" which has pierced the outermost scale of the bulb; root contraction in old bulb not indicated; leaves and roots diagrammtaic; scale = 5 cm.

PLATE 16

FIG. 14. Fifty-four- to sixty-one-day-old seedling. The cotyledon has become shriveled up and dead. As the first leaf is surrounded by the basal sheath of the cotyledon, so this second leaf sheath is surrounded by the basal sheath of the first leaf, in respect to which it is distichously placed; see Fig. 9; scale = 1 cm.

FIG. 15. Longitudinal section of thirty-one-day-old bulb; see FIG. 11; scale = 0.1 mm.

FIG. 16. Longitudinal section (not central) of thirty-one-day-old bulb; b_3 and l_3 are the points at which the primordia of the third leaf are forming; otherwise the symbols are as in preceding drawings; scale = 0 1 mm.

FIG 17. Longitudinal section (not central) of thirty-seven-day-old bulb; l_4 is the fourth leaf, not a central section; the puckered or wrinkled condition of the primary root is due to contraction, a normal phenomenon; the outlay of root tissue has a narrow slice marked off into three sections—1, 2, and 3—for details of which see FIG. 19; scale = 0.1 mm.

FIG. 18. Longitudinal section through thirty-seven-day-old seedling with a young root showing a well-differentiated root cap and primary tissues (dermatogen, periblem and pleurome); scale = 0.1 mm.

FIG. 19. Showing under high-power magnification the root tissues laid off between the numbers 1–3 in FIG. 17; for further explanation consult text; scale = 0.1 mm.

A brief conspectus of the species of Kneiffia, with the characterization of a new allied genus

Francis W. Pennell

It has recently been shown that the best-known specific name among our sundrops must be transferred from one species to another. While such a change is always peculiarly unfortunate, the desire for a definite nomenclature makes it unavoidable. In tradition the name "*fruticosa*" had been handed down as applying to the glandular-fruited element of the aggregate at first known by that name, whereas study of the Clayton Herbarium specimen upon which Linnaeus based the species showed that the name must be associated with the plant bearing on the capsule glandless incurved hairs.

Nomenclature should follow definite rules of procedure, but surely scientific truth may raise the question as to the advisability of continuing the name "*fruticosa*" for *any* species of a group of plants with herbaceous, strictly annual stems. May we not plead the right to reject a proved *nomen falsum?* Moreover, from this standpoint in freeing our most widely known *Kneiffia* from the *onus* of the word "*fruticosa*," Dr. Blake has hardly improved nomenclature—surely not in the opinion of our genetical friends—by the substitution of the name "*hybrida*." One of the incentives to the present study has been the hope of finding for this species some appropriate name.

Another incentive has been the desire to place correctly a plant characteristic of the restricted but most unique prairie near New York City, the Hempstead Plains. This plant, which seems amply distinct, appears below as *K. velutina.*

I present the results of this study with hesitation. Species-lines have not always been found clear, and in any genus so near to *Oenothera* one may expect the same tendency to split into incipient species. However, before this genus likewise is selected

for intensive cultivation and study, it may be well, from the viewpoint of the taxonomist, to present an outline of its composition.

For this study I have examined specimens in the herbaria of the New York Botanical Garden, United States National Museum, Missouri Botanical Garden, Academy of Natural Sciences of Philadelphia, University of Pennsylvania and Charleston Museum.

Stem-leaves broadly linear to ovate. Bracts similar to the leaves, linear, longer than the capsules. Stigmas linear, conspicuous. Wings of capsule pronounced. — KNEIFFIA.

- Mature capsule clavate-linear, not stipitate.
  - Hypanthium 20–25 mm. long. Sepals with spreading-hirsute caudate tips, 2–4 mm. long. Petals 20–25 mm. long. Stem, leaves and capsules hirsute. — 1. *K. pratensis.*
  - Hypanthium 10–12 mm. long. Sepals with shorter tips, strigose or somewhat spreading-pubescent. Petals 15–18 mm. long. Stem, leaves and capsules ascending- or appressed-pubescent. — 2. *K. sessilis.*
- Mature capsule-body clavate to oblong, more or less stipitate.
  - Petals of earlier flowers 12–25 mm. long. Inflorescence when in fruit much less than one half height of plant.
    - Mature capsule-body decidedly clavate, pubescent with normally incurved glandless hairs, in Nos. 8 and 9 with some interspersed gland-tipped hairs.
      - Mature capsule-body about as wide as long, usually much shorter than the stipe.
        - Capsule with minute appressed hairs. Leaves broadly linear, strigillose to glabrous. Basal leaves narrowly oblanceolate. — 3. *K. subglobosa.*
        - Capsule hirsute-strigose. Leaves linear-lanceolate, densely silvery-silky. — 4. *K. arenicola.*
      - Mature capsule-body longer than wide, longer than, about equaling or sometimes shorter than the stipe. Basal leaves broadly lanceolate to ovate.
        - Stipe and capsule-body both pubescent with glandless hairs, the

stipe frequently equaling or sometimes exceeding the capsule-body.

Stipe of capsule in fruit equaling or somewhat exceeding the permanently pubescent body.

Plant erect. — 5. *K. fruticosa.*

Plant diffusely spreading. — 5a. *K. fruticosa humifusa.*

Stipe of capsule in fruit shorter than the body, which tends to become glabrate.

Main stem-leaves 7–9 cm. long, glabrate. Capsule-body pubescent with minute hairs. — 6. *K. riparia.*

Main stem-leaves 3–6 cm. long, densely pubescent. Capsule-body pubescent with coarse hairs. — 7. *K. brevistipata.*

Stipe pubescent with gland-bearing hairs; frequently also such are interspersed with the incurved glandless hairs of the capsule-body. Stipe always shorter than the capsule-body.

Leaves nearly linear, finely pubescent to glabrate, 5–9 cm. long. Capsule-body clavate. — 8. *K. semiglandulosa.*

Leaves lanceolate, softly densely pubescent, 2–4 cm. long. Capsule-body clavate-oblong. — 9. *K. velutina.*

Mature capsule-body oblong or nearly so, pubescent with short straight gland-tipped hairs, or becoming glabrate.

Main stem-leaves linear-lanceolate to lanceolate-ovate, scarcely paler beneath. Stem pubescent to rarely glabrous. Petals of earlier flowers 18–25 mm. long.

Stem sparsely pubescent to glabrous. Leaves lanceolate.

Stipe shorter than the capsule-body. — 10. *K. tetragona.*

Stipe longer than the capsule-body. Leaves usually narrower. — 10a. *K. tetragona longistipata.*

Stem more or less hirsute. Leaves lanceolate-ovate. Inflorescence usually congested. — 10b. *K. tetragona hybrida.*

Main stem-leaves lanceolate-ovate to ovate, glaucous beneath. Stems glabrous or rarely obscurely pubescent. Petals of earlier flowers 25–30 mm. long. — 11. *K glauca.*

Petals of earlier flowers 5–15 mm. long. Inflorescence in fruit usually over one half height of plant.

Capsule pubescent with incurved glandless hairs. Petals of earlier flowers 10–15 mm. long. Inflorescence erect from the first. — 12. *K. Spachiana.*

Capsule sparsely pubescent with gland-tipped hairs. Petals of earlier flowers 5–10 mm. long. Young inflorescence nodding. — 13. *K. perennis.*

Stem-leaves filiform-linear to filiform. Bracts deltoid-ovate to ovate, shorter than the capsules. Stigmas very short, scarcely appearing as lobes. Wings of capsule ridge-like. — PENIOPHYLLUM.

KNEIFFIA Spach

Kneiffia Spach, Hist. Veg. 4: 373. 1835.
Type species, *Oenothera glauca* Michx.

1. KNEIFFIA PRATENSIS Small

Kneiffia pratensis Small, Fl. SE. U. S. 842, 1335. 1903. "Type, Jefferson Co., Mo., *Eggert*, June 11, 1878, in Herb. N. Y. B. G." Type seen.

Kneiffia Sumstinei Jennings, Ann. Carnegie Mus. 3: 480. *pl. 19.* 1906. "Dry upland field near Kittanning [Pennsylvania], D. R. Sumstine, June, 1905. Type specimens in the Pennsylvania Herbarium of the Carnegie Museum. Acc. No. 2905." Isotype seen in the herbarium of the New York Botanical Garden.

Oenothera pratensis Robinson, Rhodora 10: 34. 1908.

Prairies and woods, Ohio to Wisconsin, Iowa and Arkansas; introduced near New York City, Pittsburgh and Washington.

2. **Kneiffia sessilis** Pennell, sp. nov.

Stem 3–4 dm. tall, pubescent with ascending hairs. Leaves 6–9 cm. long, acutish, densely strigose-pubescent with ascending hairs, in age somewhat glabrate. Bracts much exceeding the

capsules. Hypanthium 10–12 mm. long. Sepals 15–16 mm. long, long-attenuate; tips more or less free in the bud. Petals triangular, 15–17 mm. long. Filaments less than one half the length of the petals. Anthers 6–7 mm. long, yellow. Stigmas becoming one half length of style. Capsule linear, at least 9 mm. long, densely pubescent with ascending to appressed hairs; not seen mature.

Type, L[ittle] R[ock], Ark[ansas], collected in flower June 2, 1885, *Dr. H. E. Hasse*; in the herbarium of the New York Botanical Garden.

Also "La. Hale," in the United States National Herbarium, with longer hypanthium, broader leaves and less dense pubescence apparently belongs to this species.

3. KNEIFFIA SUBGLOBOSA Small

Kneiffia subglobosa Small, Bull. Torrey Club **23**: 177. 1896. "North Carolina and Georgia." Type, "on the slopes or summit of Stone Mountain, De Kalb County, Georgia," collected in fruit September 6–12, 1894, *J. K. Small*, seen in the herbarium of Columbia University at the New York Botanical Garden; isotypes in the herbaria of the United States National Museum and the Missouri Botanical Garden. I have found no basis for the crediting of this species to North Carolina.

Open rocky slopes, over granite, central Georgia to central Alabama.

4. KNEIFFIA ARENICOLA Small

Kneiffia arenicola Small, Fl. SE. U. S. 842, 1335. 1903. "Type, Biltmore Herb., no. 5649d, in Herb. N. Y. B. G." Type, "sand hills, Augusta, Georgia," collected in fruit July 27, 1900, seen in the herbarium of the New York Botanical Garden; isotype in the United States National Herbarium.

Sand-hills and dry pine-barrens, in the Coastal Plain, South Carolina to southern Mississippi.

5. KNEIFFIA FRUTICOSA (L.) Raimann

Oenothera fruticosa L. Sp. Pl. 346. 1753. "*Habitat in* Virginia." Type, *Clayton 36*, is identified by Dr. S. F. Blake (Rhodora **20**: 51. 1918) as the plant here considered.

Oenothera florida Salisb. Prod. 278. 1798. New name for *O. fruticosa* L.

Oenothera linearis Michx. Fl. Bor. Amer. 1: 225. 1803. "*Hab.* in Carolina superiore." Type not seen or verified.

Kneiffia angustifolia Spach, Nouv. Ann. Mus. Par. 4: 367. 1835. "Habitat in Georgia, Carolina, et Virginia." Type not seen or verified.

Kneiffia linearis Spach, Hist. Veg. 4: 376. 1835.

Kneiffia longipedicellata Small, Bull. Torrey Club 23: 178. 1896. "West Virginia to North Carolina and Florida." Type, "Albemarle Co., Virginia," collected May 21, 1889, *W. C. Rives*, seen in the herbarium of Columbia University at the New York Botanical Garden.

Kneiffia fruticosa Raimann; Engler & Prantl, Nat. Pflanzenfam. 3^7: 214. 1893.

Oenothera longipedicellata Robinson, Rhodora 10: 34. 1908.

Open soil, sandy or barren, mostly in the Coastal Plain although extending inland upon suitable soils (as in the serpentine barrens of southeastern Pennsylvania and eastern Maryland), Long Island to Florida, Missouri and Texas.

5a. **Kneiffia fruticosa humifusa** (Allen) Pennell, comb. nov.

Oenothera fruticosa humifusa Allen, Bull. Torrey Club 1: 3. 1870. Type, "Montauk Point Long Island. [*T. F. Allen.*] July 1869," seen in the herbarium of Columbia University at the New York Botanical Garden.

Kneiffia linearis Alleni Britton, Mem. Torrey Club 5: 235. 1894. Based on *Oenothera fruticosa humifusa* Allen.

Kneiffia Alleni Small, Bull. Torrey Club 23: 177. 1894.

(?) *Oenothera linearis Eamesii* Robinson, Rhodora 10: 34. 1908. "Sandy shore of a salt pond, Stratford, Connecticut, *E. H. Eames* (type hb. Gray)." Perhaps rather a form of the species, approaching *humifusa*.

(?) *Oenothera fruticosa Eamesii* Blake, Rhodora 20: 50. 1918.

Sandy soil, eastern Long Island, New York, and perhaps on the Connecticut coast. Said to be of very distinct appearance and, locally near Montauk, to be extremely abundant. Specimens elsewhere along the coast approach the habit of this.

6. KNEIFFIA RIPARIA (Nutt.) Small

Oenothera riparia Nutt. Gen. N. Amer. Pl. 1: 247. 1818. "HAB. On the banks of Cape Fear river, Wilmington, North Carolina, in situations subject to inundation."

Kneiffia riparia Small, Fl. SE. U. S. 842. 1903.

Swamps along the Cape Fear River, near Wilmington, North Carolina. Little known, although recently re-collected by Dr. J. M. Macfarlane, C. S. Williamson, etc. Possibly not a distinct species.

7. **Kneiffia brevistipata** Pennell, sp. nov.

Stem 2–4 dm. tall, pubescent. Leaves 3–6 cm. long, linear-lanceolate, acutish, densely strigose-pubescent with ascending hairs, the young leaves very silky. Bracts slightly exceeding the capsules. Hypanthium 6–9 mm. long. Sepals 7–9 mm. long, acutish; tips not free in the bud. Petals triangular, 12–15 mm. long. Filaments about one half length of petals. Anthers 3–3.5 mm. long, yellow. Stigmas less than one half length of style. Capsule-body clavate-oblong, 5–6 mm. long; wings raised beyond ridges; pubescent, becoming glabrate, especially distally; on a stipe less than its own length.

Type, Poplarville, Mississippi, collected in flower and fruit, July 7, 1891, *S. M. Tracy 1681;* in the United States National Herbarium.

Dry pine ridges, southern Alabama to eastern Louisiana.

8. **Kneiffia semiglandulosa** Pennell, sp. nov.

Stem 3–6 dm. tall, finely pubescent, becoming glandular above, purple-red. Leaves 5–9 cm. long, lanceolate-linear, acutish, finely pubescent with ascending hairs to glabrate. Bracts much exceeding the capsules. Hypanthium 10–20 mm. long. Sepals 10–13 mm. long, acuminate; tips not or slightly free in the bud. Petals triangular, 15–25 mm. long. Filaments about one half length of petals. Anthers 5–6 mm. long, yellow. Stigmas less than one third length of style. Capsule-body clavate, 8–10 mm. long, wings exceeding the prominent ridges; finely pubescent with spreading gland-tipped, usually also with some incurved glandless, hairs, often glabrous or nearly so; on a stipe less than its own length.

Type, Biloxi, Mississippi, collected in flower April 21, 1891, *S. M. Tracy 5064,* in the United States National Herbarium.

Pine-land, West Florida to southern Mississippi; on ballast at Wilmington, North Carolina.

9. **Kneiffia velutina** Pennell, sp. nov.

Stem 2–4 dm. tall, pubescent. Leaves 2–4 cm. long, narrowly or broadly lanceolate, acute to acutish, densely soft-pubescent. Inflorescence less than one fourth height of plant. Bracts little exceeding, the upper shorter than the capsules. Hypanthium 9–12 mm. long. Sepals 10 mm. long, somewhat attenuate, so that buds are slightly caudate. Petals triangular, 15–20 mm. long. Filaments about one half length of petals. Anthers pale yellow. Stigmas about one third length of style. Capsule-body oblong, slightly clavate, 7–9 mm. long; the wings almost equaling width of body; pubescent with incurved hairs and, especially proximally, with some finer gland-tipped hairs.

Type, dry sandy soil, Garden City, Long Island, New York, collected in flower June 23, 1902, *F. A. Mulford;* in the herbarium of the New York Botanical Garden.

Dry sandy soil, apparently restricted to the Hempstead Plains of western Long Island, from which numerous collections have been seen.

10. **Kneiffia tetragona** (Roth) Pennell, comb. nov.

Oenothera tetragona Roth, Catalecta 2: 39. 1800. A garden plant, for which an American origin is stated. No specimen seen but the full description would apply to the plant here considered.

Oenothera fruticosa ambigua Nutt. Gen. N. Amer. Pl. 1: 247. 1818. "HAB. Common around Philadelphia."

Oenothera incana Nutt. *l. c.* 247. 1818. "HAB. In dry woods, Maryland.—Dr. W. C. Barton, *v. s.* in Herb. Barton."

Oenothera pilosella Raf. Ann. Nat. 15. 1820. "Indiana, near Evansville."

(?) *Oenothera canadensis* Goldie, Edinb. Phil. Jour. 6: 325. 1822. "Island of Montreal." The size of flowers would indicate that this plant must be *K. tetragona*. Apparently far out of the normal range of the species (see Macoun, Cat. Canad. Pl. 1: 172. 1883).

Oenothera ambigua Spreng. Syst. 2: 229. 1825.

Oenothera serotina Sweet, Brit. Fl. Gard. 2: *pl. 184.* 1826. A garden plant, of which no specimen seen.

Kneiffia suffruticosa Spach, Hist. Veg. 4: 374. 1835. "Croît dans les Etats Unis, depuis la Géorgie jusqu' au Canada."

Kneiffia maculata Spach, *l. c.* 375. 1835. "*Oenothera serotina* Sweet. . . ."

Oenothera fruticosa phyllopus Hook. Bot. Mag. 64: sub *pl. 3545.* 1837. "Bot. Mag. t. 332."

Oenothera fruticosa incana Hook. *l. c.* sub *pl. 3545.* 1837.

Oenothera fruticosa hirsuta Nutt.; T. & G., Fl. N. Am. 1: 496. 1840.

Oenothera hybrida ambigua Blake, Rhodora 20: 52. 1918.

Dry soil, barrens, etc., New York to Alabama, Tennessee and southern Michigan; the commonest *Kneiffia* of the Piedmont and Alleghanian floras.

10a. **Kneiffia tetragona longistipata** Pennell, var. nov.

Leaves linear-lanceolate. Stipe equaling capsule-body.

Type, woods near Clemson, Pickens County, South Carolina, collected in flower May 12, 1907, *H. D. House 3340;* in the herbarium of the New York Botanical Garden.

Piedmont Region, North Carolina to Georgia.

10b. **Kneiffia tetragona hybrida** (Michx.) Pennell, comb. nov.

Oenothera hybrida Michx. Fl. Bor. Amer. 1: 225. 1803. "*Hab.* in Carolina superiore."

Kneiffia floribunda Spach, Hist. Veg. 4: 376. 1835. "Croît dans le midi des Etats-Unis."

Mountains of North Carolina, there nearly or quite replacing the typical form of the species. As examples may be cited: *Biltmore Herb. 669b; Heller 263;* and *Standley 5366.*

11. KNEIFFIA GLAUCA (Michx.) Spach

Oenothera glauca Michx. Fl. Bor. Amer. 1: 224. 1803. "*Hab.* in sylvis remotis et occidentalibus flumini *Mississipi* confinibus, versus regionem Illinoensium." Surely the plant here considered, although not known to occur so far west as the type station.

Oenothera Fraseri Pursh, Fl. Amer. Sept. 2: 734. 1814. "In South Carolina *Fraser* . . . *v. v.* in *Hortis.*"

Kneiffia glauca Spach, Hist. Veg. 4: 374. 1835.

Kneiffia Fraseri Spach, *l. c.* 375. 1835.

Oenothera fruticosa Fraseri Hook. Bot. Mag. 64. sub *pl. 3545.* 1837.

Oenothera fruticosa glauca Lév. Monog. Onothera 107. 1902.

Wooded mountain-slopes, southern Virginia to northern Georgia, eastern Tennessee and eastern Kentucky.

12. KNEIFFIA SPACHIANA (T. & G.) Small

Oenothera Spachiana T. & G., Fl. N. Am. 1: 498. 1840. "Texas, Drummond."

Kneiffia Spachiana Small, Bull. Torrey Club **23**: 179. 1896.

Oenothera fruticosa race *Spachiana* Lév. Monog. Onothera 106. 1902.

Sandy prairies, Kansas and northwestern Arkansas to Louisiana and Texas.

13. **Kneiffia perennis** (L.) Pennell, comb. nov.

Oenothera perennis L. Syst. ed. 10, 998. 1759. Canada.

Oenothera pumila L. Sp. Pl. ed. 2. 493. 1762. "Habitat in America septentrionali."

Oenothera chrysantha Michx. Fl. Bor. Amer. 1: 225. 1803. "*Hab.* a Quebec usque ad sinum *Hudsonis.*"

Oenothera pusilla Michx. *l. c.* 225. 1803. "*Hab.* in rupibus, ad lacus *Mistassins.*"

Kneiffia chrysantha Spach, Nouv. Ann. Mus. Par. 4: 368. 1835.

Kneiffia Michauxii Spach, Ann. Sc. Nat. Bot. II. 4: 167. 1835. Based on *Oenothera chrysantha* Michx.

Kneiffia pumila Spach, Hist. Veg. Phan. 4: 377. 1835.

Oenothera pumila chrysantha Gordinier & Howe, Fl. Rensselaer Co., N. Y. 14. 1894. "Poestenkill, *Howe.*"

Oenothera pumila rectipilis Blake, Rhodora **19**: 110. 1917. "NEW BRUNSWICK: dryish rocky ground, Petit Rocher, Gloucester Co., 21 Aug. 1913, *Blake 5513* (TYPE in Gray Herb.)." The unusual state in which the pubescence is spreading may be considered as a form.

Dry fields, Nova Scotia and Quebec to Minnesota and North Carolina; northward to Hudson Bay; also on St. Pierre Island.

PENIOPHYLLUM* Pennell, gen. nov.

Slender glabrous herb, with virgately branched stem. Leaves of two forms, the basal petioled, ovate, less than 2 cm. long, the numerous stem-leaves scattered, filiform-linear to filiform, longer. Flowers in spikes terminal on the stem and branches. Bracts deltoid-ovate to ovate, shorter than the capsules. Sepals partially cohering, reflexing in two pieces. Petals about 4 mm. long, triangular. Filaments unequal, glabrous. Anthers oblong, glabrous. Style glabrous. Stigma broad, capitate, the four lobes scarcely or not distinguishable. Capsule 4–6 mm. long, ellipsoid, sharply 4-angled, not stipitate. Seeds angled, brown, 1 mm. long, irregularly clustered.

Type species, *Oenothera linifolia* Nutt.

1. **Peniophyllum linifolium** (Nutt.) Pennell, comb. nov.

Oenothera linifolia Nutt. Jour. Acad. Nat. Sci. Phila. **2**: 120. 1821. "Habitat. On the summits of arid hills and the shelvings of rocks, near the banks of the Arkansas [*T. Nuttall*]." Specimen, labeled "Arkansa, Nuttall," seen in herbarium of Columbia University at the New York Botanical Garden.

Kneiffia linifolia Spach, Nouv. Ann. Mus. Par. **4**: 368. 1835.

Kneiffia linearifolia Spach, Ann. Sc. Nat. Bot. II. **4**: 167. 1835. Based upon *Oenothera linifolia* Nutt.

Sandy soil, prairies and open woodland, southern Missouri and Kansas south to western Louisiana and eastern Texas; also on granite in central Georgia and central Alabama.

NEW YORK BOTANICAL GARDEN

* From πηνίον, thread, and φύλλον, leaf.

Preliminary note on a differential staining of the cytoplasm of Characeae

Romyn Hitchcock

The observations here recorded were made principally on two species of *Nitella*, but they are believed to apply generally for plants of this family. Perhaps the means of differential staining of living cell contents will find useful application in the study of other plants, but thus far my attention has been confined to the charas. Although it is my intention to continue observations in this direction, this should not deter others from work on the same lines. The field opened for investigation by this means is large and of much interest.

It has long been known that the peripheral layer of cytoplasm in a developed internodal cell of *Chara* is relatively dense and viscous, while that within is notably thinner. By the use of neutral red the cell contents of a *Chara* plant may be differentially stained while the plant is living. The color is readily taken up from a dilute solution. An elongated internodal cell thus stained shows the cyclosis more clearly and beautifully than in the natural condition. Observing such a stained cell there is seen a large central cylinder of a pronounced cardinal red or wine color, bordered on either side with a narrow line of green.

Within the colored cylinder, or vacuole, are numerous suspended granules, vesicles and spherical elements of various kinds, the nature of which is, for the most part, undetermined. Some of these are deeply colored and can be more advantageously studied than in the natural state. Indeed, they take the stain before the vacuole shows a general coloration. Probably these various structures have never before been so clearly seen and under such favorable conditions for study.

The borders appear green because the light passes through the marginal chloroplasts regularly arranged next to the cellulose wall. But through this green sheen may be clearly seen the outer layer

of denser cytoplasm, carrying small, uncolored granules and some spherical plasmic bodies in suspension, in active cyclosis, closely following the cell wall. This outer layer, which, for convenience, may be here specifically designated as protoplasm, is quite uncolored. Thus we have, if we imagine a cross section, the cellulose wall lined with the chloroplasts in a thin, reticulated stroma, then the thin layer of uncolored, moving protoplasm, within which is the strongly colored, wide cylinder.

The line of demarcation between the colored cylinder and the uncolored protoplasm is as sharply defined as a thin cell wall. Clearly it is the so-called vacuole wall. This line is wavy and constantly changing as it yields to the irregularities in the thickness of the protoplasm stream. The stained contents of the vacuole participate, however, in the movement of the protoplasm without, following precisely the same course. Moreover, deep within the vacuole it may be observed that the neutral or indifferent line, which marks the separation of the currents moving in opposite directions, indicates also an invisible barrier within the vacuole, which cannot be easily crossed by stray elements from the circulating stream.

A sharply defined differentiation of the cell contents has thus been effected. The significance of it is not yet clear. It is not possible at present to state precisely what particular parts or elements in the cell sap have taken the stain, or whether any color is held in solution. By far the greater number of the corpuscles or spherical elements so evident in the circulating stream of charas, are suspended in the cell sap, not in the protoplasm. The Schleimblaschen of Naegeli, later named Wimperkorperchen and mentioned by Allen as "ciliated" granules of protoplasm, are often deeply stained, but apparently not always. The name is misleading since there is no evidence of the presence of motile cilia on these bodies.

We have some admirable hypotheses concerning osmotic action in the plant cell. There are membranes permeable and selectively permeable, solutes obedient to the rules established for their guidance, whereby the whole train of physical phenomena becomes clear. It now becomes desirable to know how the coloring matter makes its way into the vacuole of the *Nitella* cell. The

solution passes directly through the outer membrane and the rotating protoplasm, without coloring or affecting them in any way, so far as can be observed. It also passes through the vacuole wall. Apparently some ingenuity will be required to explain the observed phenomenon by osmotic action. One is inclined to regard it as indicating a general permeability of the tissues to the colored solution, which happens to be one not injurious to life processes. The color is strongly held in the vacuole and in uncolored water cyclosis continues for many days.

Perhaps it is true, as some have supposed, that living protoplasm will not take up coloring matter. We are told that when the nucleus stains the cell is dead. We have seen, however, that protoplasm permits passage of the coloring matter used in these experiments. Should we, then, conclude, that the contents of the vacuole which stain so deeply are therefore dead matter? Such a view is not sustained by the observed active circulation of the colored cell sap along the definite lines established.

A PECULIAR PLASMIC STRUCTURE IN THE NITELLA CELL

Among the many corpuscular elements of the cytoplasm, of which we have almost no understanding, some are of such remarkable character as to justify particular mention, although they cannot yet be satisfactorily described. They are curious spherical masses of granular matter, of extreme plasticity, greatly varying in size up to 0.1 mm. in diameter. The granules are in a state of constant agitation, as though the mass were seething with life. Within these spheres may be seen from one to twenty or more concave, saucer-shaped disks, 5-15 μ in diameter, with contours more or less irregular, in rapid rotation, like so many wheels. They move freely about in the sphere, constantly changing the plane of rotation, sometimes on edge, sometimes lying flat but always twisting about and changing position. The nature of the movement is suggestive of cilia, but thus far none have been detected.

These have seemed to me as perhaps connected with the development of chloroplasts, many of which are found freely circulating in the cytoplasm. Although this suggestion rests upon a very weak foundation, I find it difficult to resist the impression from observations up to this time.

These structures were first observed by me on June 18, 1918, in a variety of *Nitella opaca* Ag., found at Ithaca, New York, although not recorded in the local flora. Since then I have repeatedly observed them in another species of *Nitella*, not yet seen in fruit, and also in *Chara coronata*, var. *Schweinitzii*. From this it may be inferred the structures are common to this family of plants.

The only mention I have found in the literature of anything resembling these structures is in an admirable paper by Goeppert and Cohn,* where they are rather imperfectly described, not quite as I have seen them. Doubtless the description relates to the same structures. The authors associated them with the formation of starch.

ITHACA, NEW YORK

SUPPLEMENTARY NOTE

The long, hyaline rhizoids of *Nitella* afford a more favorable means of demonstrating the selective coloring. The vacuole of a rhizoid cell becomes deeply colored, while the thin, uncolored outer stream is in active rotation.

The remarkable fact, already mentioned, that only living cells become colored, is more clearly manifest in the small and transparent rhizoid cell. In any mass of rhizoids by far the greater number will be dead cells. These remain colorless in the dye, while the living cells begin to color immediately. So long as cyclosis continues in a cell, that cell will take the color. If the cell is dying and the cyclosis is weakening it will not stain so deeply as in active life; but whenever a trace of color is seen cyclosis can be detected. When cyclosis has ceased no coloration whatever is visible. When a stained cell dies the color soon disappears from the vacuole, doubtless by diffusion in the outer water.

It would seem as though we had in this a test for living matter! But what kind of living matter has the vacuole and how does it differ from the denser, outer protoplasm? Or, have we instead, a test for vitality in a cell? Speculation as to the significance of these facts is at present unprofitable. Osmotic action affords no explanation of a concentration of a solute by passing through a

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* Ueber die Rotation des Zellinhaltes in *Nitella flexilis*. Bot. Zeit. 7: 665–673, 681–691, 697–705, 713–719. *pl. 10.* 1849.

membrane; yet, clearly, the dye is taken from the dilute, outer solution and concentrated within the walls.

With the printer's proof at hand I would like to add that the vacuole contents may be strongly colored by reason of an acid reaction. Ordinary water, or distilled water, usually is slightly alkaline, slowly changing neutral red to yellow or orange. When *Nitella* is grown in water slightly acidified with acetic acid, the vacuole becomes much more deeply colored than the culture solution.

INDEX TO AMERICAN BOTANICAL LITERATURE

1918–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Forty-one new species in various genera are described

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Zeller, S. M., & Dodge, C. W. *Arcangeliella*, *Gymnomyces*, and *Macowanites* in North America. Ann. Missouri Bot. Gard. **6**: 49–59. *f. 1–3*. F 1919.

Includes *Arcangeliella caudata*, *Gymnomyces Gardneri* and *Macowanites echinosporus*, spp. nov.

Vol. 46 No. 10

BULLETIN

OF THE

TORREY BOTANICAL CLUB

OCTOBER, 1919

Studies in the genus Lupinus—IV. The Pusilli

CHARLES PIPER SMITH

(WITH TEN TEXT FIGURES)

INTRODUCTION

In my second and third papers of this series (Bull. Torrey Club **45**: 1–22, 167–202. 1918), I treated the *Microcarpi*, the larger and more neglected division of Watson's subgenus *Platycarpos*, and I now present my review of the species and varieties properly to be included in the smaller and much less neglected group, the *Pusilli*.

The following list includes the published names that need to be considered in this paper:

L. pusillus Pursh, Fl. Am. Sept. **2**: 468. 1814.
L. brevicaulis Wats. Bot. King's Report 53. 1871.
L. Kingii Wats. Proc. Am. Acad. **8**: 534. 1873.
L. Sileri Wats. *ibid.* **10**: 345. 1875.
L. Shockleyi Wats. *ibid.* **22**: 470. 1887.
L. capitatus Greene, Pittonia **1**: 171. 1888.
L. odoratus Heller, Muhlenbergia **2**: 71. 1905.
L. scaposus Rydberg, Bull. Torrey Club **34**: 45. 1907
L. rubens Rydberg, *ibid.* **34**: 45. 1907.
L. dispersus Heller, Muhlenbergia **5**: 141. 1909.
L. flavoculatus Heller, *ibid.* **5**: 149. 1909.
L. intermontanus Heller, *ibid.* **8**: 87. 1912.
L. argillaceus Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 1913.

In my discussion of *L. malacophyllus* Greene, I indicated a disposition to question the inclusion of this species in the *Micro-*

[The BULLETIN for September (**46**: 337–388. *pl.* 14–16) was issued October 17, 1919.]

carpi, but so placed it on the basis of its verticillate inflorescence. The non-ciliate keel and the floral bracts, however, connect it with the *Pusilli*. To contrast it further with *L. subvexus transmontanus* C. P. Smith (Bull. Torrey Club 45: *f. 10*), with which it is confused, I insert here drawings of my own, FIG. 43. I now consider it better to compromise the situation by recognizing three divisions of the subgenus, and accordingly propose the following classification:

Flowers not verticillate; keel glabrous.	PUSILLI.
Flowers, at least the lower, in whorls.	
Keel glabrous; flowers 10–12 mm. long.	MALACOPHYLLI.
Keel ciliate above near claw; flowers 11–19 mm. long.	MICROCARPI

GEOGRAPHICAL DISTRIBUTION

The *Pusilli* are peculiar to western North America. Typical *L. pusillus* is primarily a species of the Atlantic drainage of the Rockies, from Alberta and North Dakota to western Kansas

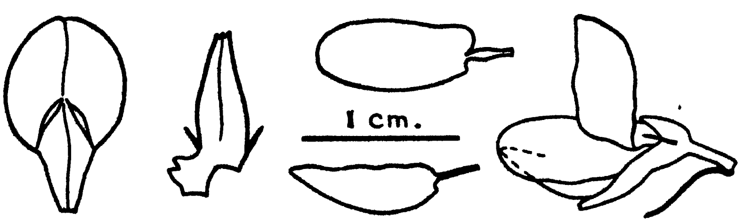


FIG. 43. LUPINUS MALACOPHYLLUS Greene. *A. A. Heller 9696* (CPS).

and New Mexico. All the other forms of the group, however, are plants of the Great Basin and Mexican Plateau, from central Washington and southwestern Wyoming to Arizona and southern California.

DIAGNOSTIC CHARACTERS

Authors' "original descriptions" are not reprinted in this paper. The diagnoses here presented have no pretense of being complete, but are intended to sum up briefly the seemingly more dependable characters. These descriptions, therefore, allow for the evident variations observed by me in the specimens listed.

The upper calyx-lip calls for special mention. While this seems to be relatively constant in size and shape in most of the forms of this group, its variability in *L. brevicaulis* should be duly

recognized. This variability parallels equal diversity in *L. subvexus* and *L. densiflorus*, as recently shown by me (Bull. Torrey Club **45**: 5. *f. 7, 16, 24, 30, 31, 35*, and *42*). In like manner, variations in length of peduncles and details of branching are not accepted by me as specific in character unless supported by recognizable differences in the floral parts or fruits. This conclusion is followed in my treatment of the variable *L. Kingii*, where these variations are evidently superficial rather than fundamental.

My measurements of the floral parts are from the softened material, mounted in water, hence should agree rather with the fresh flowers than with dried material. An allowance of about 10 per cent should be made when measurements of dried flowers are compared with my figures.

MATERIAL EXAMINED AND CITED

Seven institutions have contributed to this paper by making it possible for me to examine their specimens of this group. The names of these institutions are given below, with the respective abbreviations used in the citations. "CPS" indicates that the specimen cited is in the private collection of the writer, and "FS" indicates a specimen owned by the United States Forest Service.

B, Brooklyn Botanic Garden;
CAC, Colorado Agricultural College;
G, Gray Herbarium of Harvard University;
NY, New York Botanical Garden;
RM, Rocky Mountain Herbarium, University of Wyoming;
T, Torrey Herbarium (at New York Botanical Garden);
UC, University of California;
US, United States National Herbarium.

Key to the species and varieties of the Pusilli

Flowers usually crowded into head-like racemes.
- Stems short, seldom over 1 cm. long; leaves crowded basally; upper calyx-lip not over 2 mm. long, bifid, two-lobed or nearly obsolete. — 8. *L. brevicaulis*.
- Stems elongated, several cm. long; leaves scattered; upper calyx-lip 3–6 mm. long, bifid.
  - Pubescence copious, that of the pedicels and calyx long and spreading. — 7a. *L. Kingii*.
  - Pubescence scant, that of the pedicels and calyx short and appressed. — 7b. var. *argillaceus*.

Flowers scattered in elongated racemes.
  Flowers distinctly ascending in anthesis. — 8. [*L. scaposus.*]
  Flowers spreading in anthesis.
    Rather densely pubescent with hairs about 1 mm. long; pods smooth or scaly on the sides.
      Flowers about 6 mm. long; banner angled at apex; pods ovate, 10–15 mm. long; ovules two. — 9. *L. Shockleyi.*
      Flowers 10–12 mm. long; banner rounded at apex; pods oblong, about 20 mm. long; ovules two–four. — 10*b*. var. *pilosellus.*
    Loosely villous or varying to glabrate.
      Stems almost or quite glabrous, calyx strictly so; pods oblong, smooth or scaly on the sides, about 20 mm. long, ovules two–six; seeds 2–3 mm. across. — 10*a*. *L. odoratus.*
      Stems obviously villous, at least the lips of the calyx villous; pods usually villous on the sides; ovules mostly two.
        Racemes obviously exceeding the foliage; pods ovate, about 10 mm. long, loosely villous on the sides, seeds 2–3 mm. across.
          Branches tardily developing, the axial peduncle erect and early-flowering. — 11*a*. *L. rubens.*
          Branches early-developing, all floriferous and widely-spreading. — 11*b*. var. *flavoculatus.*
        Racemes equalled or surpassed by the foliage; pods lance-oblong, usually somewhat constricted near the middle, shaggy on the sides, about 20 mm. long; seeds about 4 mm. across.
          Flowers 10–12 mm. long; lower calyx-lip over twice as long as wide. — 12*a*. *L. pusillus.*
          Flowers 7–8 mm. long; lower calyx-lip barely twice as long as wide. — 12*b*. var. *intermontanus.*

7*a*. LUPINUS KINGII Wats. Proc. Am. Acad. 8: 534. 1873. [FIG. 44].

Lupinus Sileri Wats. *ibid.* 10: 345. 1875 (in part).

Lupinus capitatus Greene, Pittonia 1: 171. 1888.

Stems well-developed, erect with ascending branches or varying to widely spreading, 1–4 dm. tall, branched at the base or more commonly well above the base, spreading-villous; leaves usually

scattered, glabrous above or more or less hairy; peduncles variable in length, the short capitate or subcapitate racemes exceeding the foliage or surpassed by same; flowers crowded, 10–11 mm. long, commonly few; pedicels 1–2 mm. long, villous; calyx bracteolate, villous, upper lip 4–7 mm. long, bifid, the divisions slender, lower lip 5.5–7 mm. long, three-toothed; petals blue or purple, narrow, banner 8–10 mm. long, 3–5 mm. wide, usually acute at apex, wings 6–8 mm. long, 2–3.5 mm. wide, oval or oblong, keel straight, 6–8 mm. long, about 3 mm. wide; pods rhombic-ovate, about 10 mm. long; seeds about 2 × 2.5 mm.

Watson soon recognized the affinity of his supposed perennial, *L. Kingii*, and his annual, *L. Sileri*, and reduced the latter to synonymy. This viewpoint has been followed by Coulter (Man. Bot. Rocky Mts. 273. 1885), Coulter and Nelson (New Man. Rocky Mt. Bot. 469. 1909), Rydberg (Fl. Colo. 100, 1906; Fl.

FIG. 44. LUPINUS KINGII Wats. 1. *Korstion & Baker 131* (FS); 2. *C. A. Purpus 8083* (US); 3. *S. Watson 234* (US); 4. *C. F. Baker 439* (US); 5. *M. E. Jones 5641* (US).

Rocky Mts. 469. 1917), and Heller (Muhlenbergia 6: 71. 1910). Heller and Rydberg have also referred Greene's *L. capitatus* to Watson's species. Wooton and Standley (Contr. U. S. Nat. Herb. 19: 340. 1915), however, have recognized *L. Kingii* and *L. Sileri* as distinct species, each represented in New Mexico, and have segregated *L. argillaceus* as a new species. My study of the specimens listed below prevents my recognition of more than one species here, though as least one variety probably deserves attention. I can not see specific characters in the variations in length of peduncles, or in the extremes of types of branching (widely divaricate to ascending) here; but the more sharply defined variation in pubescence seems to be of sufficient definition for use in varietal recognition. Greene attributes to *L. capitatus*

an "entire" lower calyx-lip; but the several Coconino County specimens examined by me have the normal three-toothed lower lip.

UTAH. Beaver County: Beaver, Aug., 1882, *M. E. Jones* (G). Garfield County: Panguitch Lake, 7 Sept., 1894, *M. E. Jones 60151* (US). Piute County: Grass Valley, *L. F. Ward 648* (US); Grass Valley, Aug., 1882, *Powell Exped., L. F. Ward* (G). San Juan County: mesa east of Monticello, July, 1911, *P. A. Rydberg & A. O. Garrett 9214* (US, NY). Sevier County: Burrville, July, 1894, *M. E. Jones 5641* (US, RM); Loa Pass, July, 1894, *M. E. Jones 5641* (NY, UC); Fish Creek Canyon, July, 1909, *A. O. Garrett 2532* (NY). Summit County: Parley's Park, July, 1869, *S. Watson 234* (US). County not given: 1872, *Capt. Bishop* (US); Juniper Mountains, 1898, *C. A. Purpus 6256* (US).

COLORADO. Archuleta County: Piedra, July, 1899, *C. F. Baker 439* (G, NY, RM, US); Pagosa Springs, Aug., 1904, *E. O. Wooton* (US). Costilla County: Garland, July, 1896, *C. L. Shear 3682* (NY); San Acacio, Culebra Creek, July, 1912 *E. R. Warren* (RM). Delta County: without definite locality, June, 1892, *J. H. Cowen* (US). Gunnison County: Gunnison Watershed, July, 1901, *C. F. Baker 452* (G, NY, RM, UC, US). LaPlata County: Durango, July, 1896, *F. Tweedy 452* (US). LaPlata or Montezuma County: Parrott City, Rio Mancos trail July, 1875, *Hayden Survey 1197, T. S. Brandegee* (UC); trail, between Rio de los Mancos and Rio la Plata, July, 1875, *T. S. Brandegee* (G); Thompsons Park, LaPlata Mountains, July, 1898, *C. F. Baker, F. S. Earle, & S. M. Tracy 441* (G, NY, UC, US). County not given. Colfax Sept., 1877, *T. S. Brandegee* (UC); 1896 *F. Clements 318* (NY).

NEW MEXICO. Bernalillo County: Tijeras, Sandia Mountains, May, 1914, *C. C. Ellis 430* (US). Dona Ana County: Organ Mountains, May, 1905, *E. O. Wooton* (RM). Grant County: GOS Ranch, Aug.–Sept., 1911, *J. M. Holzinger* (US). McKinley County: Cooledge [Guam], July, 1889, *M. Hopkins* (US). Rio Arriba County: vicinity of Chama, July, 1911, *P. C. Standley 6793* (US); Dulce, Jicarilla Apache Reservation, Aug., 1911, *P. C. Standley 8071* (US); El Rito, Aug., 1904, *E. O. Wooton* (US). Sandoval County: Rito de las Frijoles, Aug., 1902, *T.*

D. A. Cockerell 19 (US); Rito de las Frijoles, Aug., 1910, *W. W. Robbins* (RM). San Juan County: Tunitcha Mountains, Aug., 1911, *P. C. Standley 7786* (US). Socorro County: Mogollon Mountains, middle fork of the Gila, Aug., 1900, *E. O. Wooton* (US); Wheelers Ranch, July, 1906, *E. O. Wooton* (RM, US).

ARIZONA. Apache County: White Mountains, Aug., 1903, *D. Griffiths 5273* (US); Alpine, July, 1912, *L. N. Goodding 1258* (RM). Cochise County: Bisbee, July, 1912, *L. N. Goodding 1258* (US). Coconino County: Cosnino, July, 1883, *H. H. Rusby* (US); Flagstaff, Aug., 1884, *M. E. Jones 3947* (NY, RM, US); San Francisco Mountains, 2 Sept., 1889, *F. H. Knowlton 174* (US); Flagstaff, June, 1892, *J. W. Toumey 573* (US); Grand Canyon, July, 1892, *J. W. Toumey 575* (G, US); Grand Canyon, July, 1892, *E. O. Wooton* (US); Flagstaff, Sept., 1895, *J. W. Toumey* (NY, UC); Flagstaff, July, 1897, *C. L. Harris 913* (US); Flagstaff, 1900, *C. A. Purpus 8083* (US); Flagstaff, June, 1901, *J. B. Leiberg 5522* (US); Flagstaff to Mugillo Mountains, July, 1903, *D. Griffiths 4974* (US); Coconino Forest, Aug., 1908, *G. A. Pearson 11* (US); Grand Canyon, July, 1912, *V. Rattan* (UC); Grand Canyon, June, 1913, *A. E. Hitchcock 39* (US); Flagstaff, Aug., 1915, *A. S. Hitchcock* (US); Kaibab Forest, 1918, *Korstion & Baker 131* (FS). Navajo County: Taylor, June, 1897, *W. Hough 72* (US). Pima County: Sabina Canon, Catalina Mountains, Apr., 1892, *J. W. Toumey 572* (US 211833 in part). Yavapai County: Ashfork, July, 1903, *D. Griffiths 4873* (US). County not determined: Hell's Canyon, May, 1883, *H. H. Rusby 1402* (US); Hell's Canyon, June, 1883, *H. H. Rusby 552, 554* (UC); Nagles Ranch, 13 Sept., 1894, *M. E. Jones 6054g* (US).

7*b*. **Lupinus Kingii argillaceus** (Woot. & Standl.) comb. nov. [FIG. 45.]

Lupinus argillaceus Woot. & Standl. Contr. U. S. Nat. Herb. **16**: 137. 1913.

Differs from the typical form of the species in the pubescence being shorter and subappressed, especially that of the calyx and pedicels being appressed and inconspicuous. No other characters seem to separate this from the widely branching individuals of the obviously villous species.

NEW MEXICO. San Miguel County: near Pecos, Aug., 1908, *P. C. Standley 4974, 4975* (NY, US). McKinley County: Rio Zuni, July, 1892, *E. O. Wooton* (US 735190 and 562216).

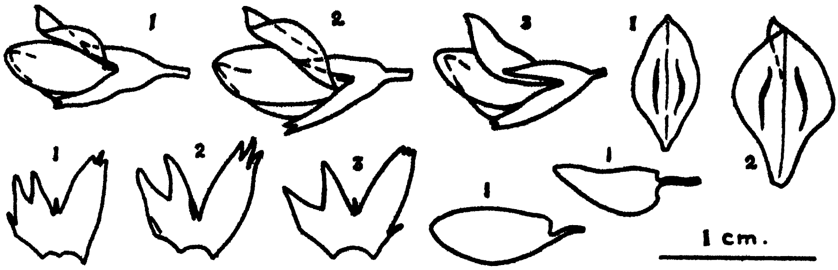


FIG. 45. LUPINUS KINGII ARGILLACEUS (Woot. & Standl.) C. P. Smith. 1. *P. C. Standley 4975* (US); 2. *E. O. Wooton* (US 562216); 3. *J. Wolf 195* (US).

COLORADO. Mesa County: Loma, Rio Grande, Sept., 1873, *J. Wolf 195* (US).

8. LUPINUS BREVICAULIS Wats. Bot. King's Report 53. 1871. [FIG. 46.]

Lupinus dispersus Heller, Muhlenbergia 5: 141. 1909.

Lupinus scaposus Rydberg, Bull. Torrey Club 34: 45. 1907.

Low, less than 1 dm. tall, densely villous, stems short, seldom over 1 cm. long; leaves crowded basally, glabrous above: peduncles 3–6 mm. long, the subcapitate racemes about 2 mm. long, commonly elongating after anthesis; flowers 6–8 mm. long, crowded; pedicels 1–2 mm. long, villous; calyx bracteolate, villous, upper lip 1–2 mm. long, truncate, two-lobed or bifid, lower lip 4–6 mm. long, two- to three-toothed, or rarely entire; petals bright blue or pale-tinted, banner about 6 mm. long, 2–4 mm. wide, apex angled or rounded, wings 4–6 mm. long, 2 mm. wide, keel 4–6 mm. long, straight; pods ovate, about 10 mm. long, ovules two or three, seeds 2 mm. long.

From the first I experienced difficulty in attempting to follow others in separating *L. brevicaulis* and *L. dispersus*. Careful attention to the original descriptions shows few differences brought out, except as to the calyx-lips.

Quoting from Watson:

. . . upper lip very short, truncate, obsoletely toothed, membranous, lower entire or obscurely toothed. . . .

Quoting from Heller's description of his species:

. . . upper calyx lobe less than 2 mm. long, 2-parted almost to the base, the divisions with a broad somewhat U-shaped sinus; lower lobe nearly 4 mm. long, prominently 2-toothed, the sinus narrow. . . .

I have dissected flowers and made drawings from fourteen of the numerous collections examined and here listed. As shown in FIG. 44, both the lower and upper calyx-lips exhibit considerable

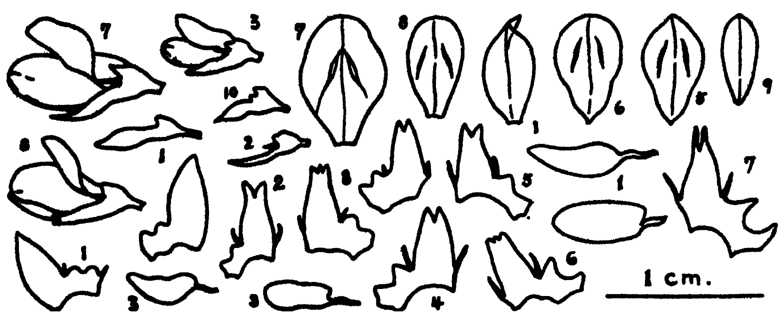


FIG. 46. LUPINUS BREVICAULIS Wats. 1. *A. A. Heller 8646* (US); 2. *M. E. Jones 3814* (US); 3. *Mrs. J. Clemens* (CPS); 4. *M. E. Jones 5273* (US); 5. *M. E. Jones 5139y* (US); 6. *M. E. Jones 5272b* (US); 7. *D. Griffiths 3955* (US); 8. *E. O. Wooton* (US 737532); 9. *C. F. Baker 437* (US); 10. *J. B. Leiberg 2198* (US).

variation. The lower lip is entire in only one of these fourteen cases, i.e. Heller's Reno collection. Five cases show a three-toothed lower lip, four cases the two-toothed condition, and two collections show both two-toothed and three-toothed individual calyces.

Rydberg's *L. scaposus* is evidently a pathological phase of *L. brevicaulis*. I have examined the type collection (T, G, RM) and cannot find justification for recognizing this form even as a variety. Three other collections, from as many states, include specimens of this variation. These are: "Jones 5273, Kanab, Ut." (RM 14246); "Lemmon, Camp Lowell, Ari." (G); and "Watson 223, Coyote Mts., Nev." (T). We should not overlook Watson's own record (1871, p. 53) which reads:

A form of this was collected with some of the peduncles much elongated and bearing above the leaves loose racemes of reduced florets, apparently perfect in all their parts, but usually sterile (223).

I see only the one species in this series of specimens. If the extremes of western Nevada were alone before me, I could readily accept Heller's segregate as a variety of Watson's species; but

careful study of all the material considered shows no sufficiently constant or fundamental differences available for a satisfactory varietal classification.

OREGON. Lake County: Chewaucan Marsh, 2 June, 1911, *W. W. Eggleston 6771* (US); Fifteen Mile Creek, Warner Valley, 16 June, 1911, *W. W. Eggleston 6983* (US). Harney County: base of Steins Mountain, 30 May, 1885, *T. Howell* (US, G). Malheur County: Barren Valley, 1885, *W. Cusick 1250* (US); Dry Creek hills, June, 1901, *W. Cusick 2554* (US, G, NY, UC, RM); Barren Valley, June, 1896, *J. B. Leiberg 2198* (US, G, UC).

NEVADA. Humboldt County: Coyote Mountains, June, 1868, *S. Watson 223* (US 41363, T); Humboldt Valley, 1868, *S. Watson 222* (T). Washoe County: Reno hills, June, 1900, *S. G. Stokes* (NY); Truckee Pass, June, 1906, *P. B. Kennedy 1333* (US, NY); Truckee Pass, June, 1907, *A. A. Heller 8646* (US, B); Reno, 1 May, 1910, *A. A. Heller 10006* (US, B, NY, RM). Mineral County: Hawthorne, June, 1882, *M. E. Jones 3814* (US, NY). Esmeralda County: Candalaria, *W. H. Shockley 51* (UC). Nye County: Tonopah, June, 1907, *W. H. Shockley 86* (UC); Rhyolite, June, 1907, *W. H. Shockley 54* (UC). Lincoln County: Caliente, May, 1902, *L. N. Goodding 942* (RM).

UTAH. Weber County: Ogden, June, 1903, *S. G. Stokes* (US). Davis County: Antelope Island, June, 1869, *S. Watson 222* (US). Salt Lake County: near Garfield, May, 1909, *Mrs. J. Clemens* (US, NY, RM, CPS). Juab County: Diamond Valley, 28 Apr., 1894, *M. E. Jones 5125c* (US). Piute County: Marysvale, May, 1894, *M. E. Jones 5338i* (US). Washington County: La Verken, May, 1894, *M. E. Jones 5183b* (US); Silver Reef, May, 1894, *M. E. Jones 5149g, 5151* (US); Santa Clara Valley, Apr., 1894, *M. E. Jones 5139h, 5139y* (US); Spring Dale, May, 1894, *M. E. Jones 5261h* (US). Kane County: Kanab, May, 1894, *M. E. Jones 5273* (US, NY, UC, RM).

COLORADO. Garfield County: Glenwood Springs, June, 1899, *G. E. Osterhout* (T, G, RM). Delta County: Surface Creek, March, 1892, *C. A. Purpus 175* (UC); Hotchkiss, June, 1802, *J. H. Cowen 147* (NY, G); same, *J. H. Cowen 648* (CAC); Delta, June, 1909, *L. Tidestrom 2198* (US). Montrose County: Naturita, May, 1914, *E. Payson 306* (NY, RM). La Plata County: Dur-

ango, June, 1898, *C. S. Crandall* (RM). Archuleta County: Arboles, June, 1899, *C. F. Baker 437* (US, G, NY, UC, RM).

NEW MEXICO. McKinley County: Fort Wingate, 1883, *W. Mathews* (G). Socorro County: Patterson, June, 1892, *E. O. Wooton* (US 241178, US 737533). Dona Ana County: plains at base of Organ Mountains, 1852, *C. Wright 1362* (US 20950-2); Filmore Canyon, Organ Mountains, May, 1905, *E. O. Wooton* (US). Grant County: Copper Mines, June, 1851, *Mex. Bound. Survey 287* (NY); River Mimbres, May, 1851, *G. Thurber 335* (T); Silver City, 1891, *G. C. Nealley 39* (NY); same, *G. C. Nealley 40* (US); Silver City, May, 1906, *V. Bailey* (US). County not given: without definite locality, 1869, *E. Palmer* (US 20576, T): Mesa Top, 1883, *C. D. Walcott 28* (US).

CHIHUAHUA. Ojo de Vacate, June, 1851, *G. Thurber 335* (NY).

ARIZONA. Cochise County: Camp Lowell, 1880, *J. G. Lemmon* (G). Santa Cruz County: Tumacacori and vicinity, 1903, *D. Griffith 3955* (US). Pima County: Canaca to Arivaca, 1903, *D. Griffith 3570* (US). Yavapai County: Ash Fork, May, 1903, *D. Griffith* (US). Coconino County: base of San Francisco Mountains, July, 1884, *J. G. Lemmon & wife* (US, UC); Hell's Canyon, May, 1883, *H. H. Rusby 554* (US, T); Turkey Tanks, Flagstaff, June, 1891, *D. T. McDougal* (US); Pipe Spring, May, 1894, *M. E. Jones 5272b* (US). Mohave County: Hackberry, May, 1884, *M. E. Jones* (US 220209); near Kingman, June, 1893, *N. C. Wilson* (UC).

CALIFORNIA. San Bernardino County: New York Mountains, near Leastalls, June, 1915, *S. B. Parish 10259* (UC). Inyo County: Bishop Creek, May, 1886, *W. H. Shockley 424* (UC).

9. LUPINUS SHOCKLEYI Wats. Proc. Am. Acad. **22**: 470. 1887. [FIG. 47.]

More or less acaulescent, 1-2 dm. tall, densely pubescent with hairs about 1 mm. long, spreading on the stems and petioles, sub-appressed on the leaves; peduncles 5-10 cm long, racemes lax, 3-6 cm. long, equalled or surpassed by the foliage; flowers about 6 mm. long; pedicels slender, often curved, about half as long as the flowers, spreading-pubescent; calyx hairy, the upper lip 3 mm. long, bifid, lower lip 3-4 mm. long, minutely three-toothed or

sometimes bifid; petals "blue or purple" or pink, banner 5–6 mm. long, 4 mm. wide, angled at apex, wings 5 × 3 mm., keel straight, 4 mm. long, 2 mm. wide: pods "oblong ovate," ciliate on the margins, scaly on the sides, ovules two, seeds rough, about 3 mm. in diameter, pale in color.

ARIZONA. Mohave County: Kingman, May 1884. *J. G, Lemmon & wife* (UC).

NEVADA. Esmeralda County: Sodaville, *W. H. Shockley 367* (T, UC); same locality, June, 1888, *W. H. Shockley 4359* (NY)· Mineral County: Hawthorn, June, 1882, *M. E. Jones 3812* (NY, RM, US).

CALIFORNIA. Kern County: Tehachapi, June, 1884, *K. Brandegee* (UC). Riverside County: Palm Springs, Apr., 1905, *H. M. Hall 5762* (UC); Point of Rocks, Whitewater, Apr., 1911,

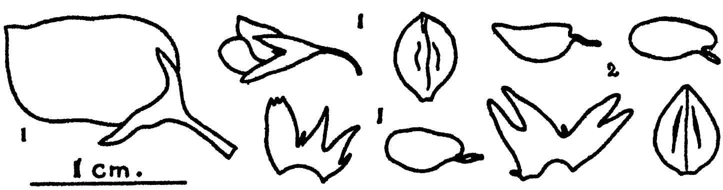


FIG 47. LUPINUS SHOCKLEYI Wats 1 *M E Jones 3812* (US), 2 *J G Cooper* (US 344389)

E. E. Schellenger (UC). San Bernardino County: Camp Cady, Mojave River, June, 1861, *J. G. Cooper* (US); Browns Ranch, Mojave Desert, May, 1882, *S. B. Parish* (UC); Morongo, Colorado Desert, March, 1882, *S. B. Parish 1270* (NY; from the herbarium of H. E. Hasse); Mojave River, *E. Palmer* (NY; from the herbarium of P. V. Le Roy); Barstow, *K. Brandegee* (UC); Daggert, May, 1917, *K. Brandegee* (UC); Kelso, May, 1917, *K. Brandegee* (UC); Colorado Desert, Apr., 1905, *T. S. Brandegee* (UC). San Diego County: Borregos Spring, *T. S. Brandegee* (UC).

The New York sheet from Dr. Hasse's herbarium (*S. B. Parish 1270*) includes two specimens of *L. Shockleyi* and one specimen each of *L. odoratus*, *L. concinnus*, and *L. microcarpus* var. *ruber*. Mr. Parish informs me that his No. 1270 belongs to a collection of *L. odoratus* taken in May, 1882, while his visit to the Morongo was in April of that year. It seems evident, therefore, that this label cannot be accepted as correctly applying to any of the

specimens assembled on the sheet. The boundary line separating Riverside and San Bernardino Counties passes through the Morongo country and it seems to be impossible to determine on which side of the line were taken the Morongo specimens here referred to San Bernardino County.

Palmer's specimen from Le Roy's herbarium is a striking variation towards *L. odoratus* and probably should have been given more serious attention here.

10a. LUPINUS ODORATUS Heller, Muhlenbergia 2: 71. 1905. [FIG. 48.]

Nearly or quite acaulescent, glabrous or sparsely villous, 1–2 dm. tall; peduncles commonly erect, equalling or exceeding the leaves, racemes 5–8 cm. long; flowers 10 mm. long, well-scattered; pedicels 4–6 mm. long, glabrous; calyx glabrous, upper lip about as broad as long, 2 mm. long, entire or notched, lower lip about 5 mm. long, entire or obscurely three-toothed; petals blue or purple, the banner with a yellow center, 10 mm. long and 10 mm. wide, wings 8 mm. long, 5–6 mm. wide, keel 7–8 mm. long, the point decidedly upturned; pods oblong, 17–20 mm. long, smooth or scaly on the sides, villous on the margins, ovules two to six, seeds rough, about 3 mm. across, unmarked (?).

FIG. 48. LUPINUS ODORATUS Heller. 1. *S. B. Parish 4057* (US); 2. *A. E. D. Elmer 3624* (US); 3. *A. A. Heller 8207* (CPS).

This excellent species is of special interest both because of its number of ovules and its limited supply of hair-covering. The former character suggests relationship to certain species of the annuals of the subgenus *Lupinus*; but its cotyledons are sessile and its relationship is evidently closer to *L. pusillus*. There should be no further excuse for confusing it with *L. brevicaulis*.

CALIFORNIA. Los Angeles County: Dry Lake, Antelope Valley, May, 1896, *J. B. Davy 2223* (UC); Lancaster, June, 1902,

A. E. D. Elmer 3624 (B, G, NY, US); Lancaster, May, 1909, *K. Brandegee* (UC). Kern County: Antelope Valley, May, 1905, *F. Grinnell* (US); North Fork Kern River, June, 1888, *E. Palmer 112* (US); Green Horn Mountains, June, 1888, *E. Palmer 112* (T); near Randsburg, May, 1906, *H. M. Hall & H. P. Chandler 7285* (UC); Randsburg, May, 1913, *K. Brandegee* (UC). San Bernardino County: Fort Mojave, *J. G. Cooper* (US); Cajon Pass, east slope, June, 1861, *J. C. Cooper* (US); Mojave River, June, 1876, *E. Palmer 84* (G); Mojave Desert borders, May, 1882, *S. B. & W. F. Parish 96* (T), *1269* (G); Mojave Desert, May, 1899, *C. J. Pringle* (G, US); Hesperia, June, 1901, *S. B. Parish 4957* (NY, US); same locality, May, 1892, *S. B. Parish 2354* (T); same locality, June, 1895, *S. B. Parish 3774* (G, UC); Mojave, Apr., 1905, *Mrs. C. DeKalb* (NY); Barstow, May, 1905, *H. M. Hall 6166* (B, UC); five miles west of Barstow, March, 1914, *Mable Minthorn* (UC); Kramer, Apr., 1905, *A. A. Heller 7673* (B, NY, UC); same locality, May, 1909, *K. Brandegee* (RM, UC); same locality, 1919, *K. Brandegee* (UC); Blacks Ranch, near Fremont Peak, May, 1906, *Hall & Chandler 6843* (B, G, UC); Deadman's Point, Apr., 1916, *S. B. Parish 10787* (UC). Inyo County: near Olancha, Apr., *T. S. Brandegee* (UC); Owens Lake, Apr., 1900, *S. W. Austin 22* (NY); Laws, May, 1906, *A. A. Heller 8207* (B, G, NY, UC); Big Pine, June, 1906, *Hall & Chandler 7285* (RM, UC).

NEVADA. County not given: Great Basin, 1875, *J. G. Lemmon* (US 20973). Washoe County: without definite locality, May, 1875, *J. G. Lemmon* (G).

ARIZONA. Mohave County: near Kingman, June, 1884, *J. G. Lemmon* (G); Hackberry, May, 1884, *M. E. Jones 66* (G).

10*b*. **Lupinus odoratus pilosellus** var. nov.

A *L. odorati* differt caulibus petiolisque conspicue pilosis: leguminibus oblongis, 2 cm. longis; seminibus 2–4.

Stems and petioles conspicuously pilose with short white spreading hairs; pods oblong, 2 cm. long, two- to four-seeded.

CALIFORNIA. San Bernardino County: Nipton, June, 1905, *K. Brandegee* (Type, UC 180117); Mohave River, May, 1876, *E. Palmer 84* (UC 82240).

11a. LUPINUS RUBENS Rydberg, Bull. Torrey Club **34**: 45. 1907. [FIG. 49.]

Branched at or near the base, 6–15 cm. tall, villous, axial peduncle usually erect, commonly flowering before the branches develope, racemes exceeding the foliage; flowers 6–12 mm. long, approximate or well scattered; pedicels 1–2 mm. long, usually glabrous but sometimes more or less villous; calyx-lips setose-villous, the cup commonly free of hairs, upper lip entire or notched, lower lip entire or two- or three-toothed; petals as in *L. odoratus*, the banner with a yellow center; pods ovate, 8–12 mm. long, usually two-seeded, more or less villous on the sides; seed characters yet to be determined.

This is a variable species intermediate between *L. pusillus* and *L. odoratus*. One extreme, when in flower, is hardly separable from the New Mexican variation of *L. pusillus*, while other forms approach closely to *L. odoratus*. Critical cases will evidently have to be judged in terms of fruiting material.

FIG. 49. LUPINUS RUBENS Rydberg. 1. *M. E. Jones 5138* (US); 2. *M. E. Jones 4413* (US); 3. *M. E. Jones 5024t* (US); 4. *E. D. Ball* (CPS); 5. *J. G. Cooper* (US 344379).

UTAH. Emery County: Green River, May, 1890, *M. E. Jones* (US); same locality, May, 1909, *E. D. Ball* (CPS). Grand County: Grand River Canyon below Moab, July, 1911, collector not given (NY). Kane County: Kanab, *Mrs. A. P. Thompson* (G). Washington County: St. George, Apr., 1880, *M. E. Jones 1657* (NY, RM, T, US); same locality, Apr., 1884, *M. E. Jones 5110j* (US); Santa Clara Valley, Apr., 1884, *M. E. Jones 5138* (NY, UC, US). County not ascertained: southern Utah, 1872,

Capt. Bishop (US), 1873, *Capt. Bishop* (G), 1874, *C. C. Parry 4, 42* (T).

ARIZONA. Navajo County: six miles northeast of Winslow, May, 1901, *L. F. Ward* (US). Coconino County: ten miles north of Tuba, May, 1901, *L. F. Ward* (US). Mohave County: Hackberry, May, 1884, *M. E. Jones 4413* (US). County not determined: no locality, 1869, *E. Palmer* (US 20944, two upper specimens); Beaverdam, Apr., 1894, *M. E. Jones 5024i* (US).

NEVADA. Clark County: Cottonwood Springs, Vegas Valley, 1891, *V. Bailey 1876* (US). Lincoln County: Caliente, Meadow Valley Wash, May, 1902, *L. N. Goodding 942* (RM). County not given: Dry Lake, Apr., 1905, *L. N. Goodding 2234a* (G, NY, RM, UC).

CALIFORNIA. Inyo County: Wild Rose Springs, Panamint Mountains, May, 1915, *S. B. Parish* (UC). San Bernardino County: Cajon Pass, 1860–1861, *J. G. Cooper* (RM, left-hand specimen); Providence Mountains, near summit, May, 1861, *J. G. Cooper* (US); New York Mountains, June, 1915, *S. B. Parish 10073* (UC); Good Springs, May, 1915, *K. Brandegee* (UC); Cima Station, May, 1915, *K. Brandegee* (UC 180152, upper specimen).

11*b*. **Lupinus rubens flavoculatus** (Heller) comb. nov. [FIG. 50.]

Lupinus flavoculatus Heller, Muhlenbergia 5: 149. 1909.

Differs from *L. rubens* proper in the early development of floriferous, widely spreading branches, in the longer pedicels (1–4 mm.), and in the lower calyx-lip being usually two-toothed.

This much resembles various specimens of *L. odoratus*, but seems to be fairly constant in its differences as to pubescénce and fruit. It varies easily into that variable species, and my disposition of some of the specimens cited here is not beyond fair questioning. One of the specimens (UC 149911) is evidently a pathological variation.

NEVADA. Nye County: Rhyolite, May, 1907, *W. H. Shockley 43* (UC); Rhyolite, May, 1909, *A. A. Heller 9669* (B, NY, RM, UC, CPS).

CALIFORNIA. Inyo County: Darwin Mesa, Yucca Valley, May, 1891, *F. V. Coville & F. Funston 877* (US); Boundary Canyon, Grapevine Mountains, June, 1891, *F. V. Coville & F. Funston 977* (G, T, US); Lone Pine, May, 1913, *K. Brandegee* (UC).

San Bernardino County: Barnwell, May, 1911, *K. Brandegee* (UC 149898, 149909–10–11); Cima Station, May, 1915, and

FIG. 50. LUPINUS RUBENS FLAVOCULATUS (Heller) C. P. Smith. *A. A. Heller 9669* (CPS).

June, 1915, *K. Brandegee* (UC). Kern County: South Fork Kern River, 1898, *C. A. Purpus 5714* (UC, US). Modoc County: Surprise Valley, May, 1879 *J. G. Lemmon* (G).

12*a*. LUPINUS PUSILLUS Pursh, Fl. Am. Sept. 2: 468. 1814. [FIG. 51.]

Stems well-developed, branches ascending to widely-spreading, loosely villous, 1–2 dm. tall; peduncles 1–2 cm. long, racemes 3–5 cm. long, mainly equalled or exceeded by the leaves; flowers 10–12 mm. long, well scattered; pedicels about 2 mm. long, villous; calyx villous, upper lip broader than long, 2 mm. long, the short teeth acute or rounded, lower lip over twice as long as wide, 5–6 mm. long, the apex entire and acuminate, acute, or rounded, or occasionally three-toothed; petals bluish, purplish, or almost

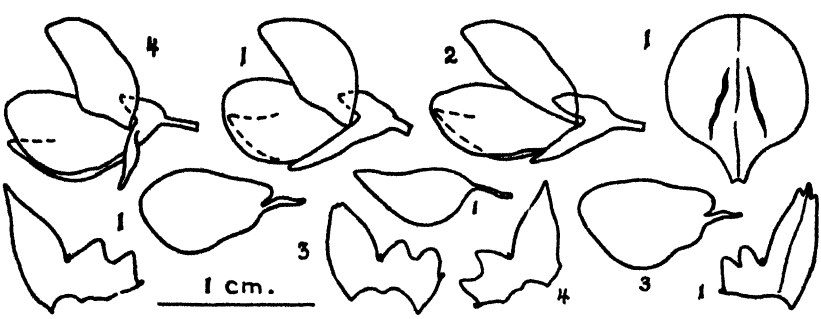


FIG. 51. LUPINUS PUSILLUS Pursh. 1. *V. Bailey 10* (US); 2. *M. E. Moodie 946* (US); 3. *A. Nelson 8258* (US); 4. *E. Palmer 82* (US 291129).

white, banner 10–11 mm. long and 9–10 mm. wide, wings 8–9 mm. long, 5–6 mm. wide, keel 8 mm. long, 3.5 mm. wide, the point somewhat upturned; pods 20–25 mm. long, lance-oblong, acute at the apex, slightly constricted near the middle, two-seeded; seeds about 4 mm. across, rugose, apparently unmarked.

The typical form of this species is mainly confined to the Atlantic drainage of the Rocky Mountain region, the exception being its occurrence on the "Snake Plains" of southern Idaho. The New Mexican plants referred here may prove to be a separable variety, as the racemes often exceed the foliage and the plants suggest the larger phases of *L. rubens*. Fruiting material, with matured seeds, is much desired from New Mexican localities and Green River, Utah. The Great Basin form, separated by Heller, deserves recognition as a variety, some intermediates occurring.

ALBERTA. Bow Valley County: West Fork Water Coulee, near Rosedale, June, 1915, *M. E. Moodie 946* (G, US). Medicine Hat County: Medicine Hat, May, 1894, *J. Macoun 4069* (G).

ALBERTA or SASKATCHEWAN. West of South Saskatchewan, June, 1879, *J. Macoun 104* (G); north of Cypress Hills, Aug., 1880, *J. Macoun* (T); Cypress Hill, July, 1895, *J. Macoun 10412* (G).

IDAHO. Elmore County: King Hill, July, 1911, *Nelson & McBride 1111* (RM). Ouyhee County: Murphy, July, 1911, *Nelson & McBride 1030* (RM). Bingham County: Blackfoot, July, 1893, *E. Palmer 275* (US). Lincoln County: Bluelakes, June, 1893 *E. Palmer 82* (US).

MONTANA. Cascade County: Great Falls, July, 1885, *R. S. Williams 214* (US); Great Falls, Sept., 1886, *F. W. Anderson* (UC); Falls of the Missouri, July, 1887, *F. W. Anderson 1422* (NY). Dawson County: near Glendive, 1883, *L. F. Ward* (US); Glendive, June, 1908, *B. T. Butler 2005, 2006* (NY). Still Water County: Still Water, July, 1889, *F. Tweedy 3* (NY). Custer County: Miles City, June, 1893, *F. E. Lloyd* (NY). Yellowstone County: Custer, May, 1890, *J. W. Blankinship* (UC). Park County: Upper Yellowstone, July, 1899, *J. W. Blankinship* (G, RM). Locality not given: 1890, *P. A. Rydberg 397* (NY); June, 1890, *J. W. Blankinship 156* (US).

YELLOWSTONE PARK. Yellowstone, *V. Havard* (US); eleven miles above Glendive, July, 1883, *L. F. Ward* (US); mouth of Gardiner River, *F. Tweedy* (US).

WYOMING. Albany County: Laramie River, Laramie Peak, 1864, *R. B. Hetz* (US). Converse County: Lost Springs, July, 1915, *W. L. Hees 113* (RM). Crook County: Pine Ridge, July,

1909, *M. Cary 365* (US). Diobrara County: Van Tassell, Douglas, June, 1899, *H. M. Barrow 35* (RM). Johnson County: Buffalo, 23 July and 26 July, 1898, *T. A. Williams* (US). Laramie County: Fairbanks, July, 1894, *A. Nelson 490* (G, RM, T, UC, US). Natrona County: Alcova, July, 1901, *L. N. Goodding 157* (RM). Platte County: Wheatland, June, 1901, *A. Nelson 8258* (B, G, NY, RM, UC, US). Washakie County: Worland, June, 1909, *B. C. Buffum* (RM). County not given: 1893, *B. W. Evermann* (US); four miles below U. L. Ranch, July, 1896, *F. H. Knowlton 159* (US); Sweetwater River, July, 1898, *E. Nelson 4989* (CAC, RM); Cheyenne River, *E. J. Wallace* (RM).

COLORADO. Denver County: Denver, May, 1873, *J. M. Coulter* (US); Denver, June, 1873, *J. Wolf 20* (US); Denver, Platte River, June, 1878, *M. E. Jones 199* (NY); Denver, July, 1885, *G. W. Letterman* (US). Fremont County: Canon City, 1872–1873, *T. S. Brandegee* (UC). Larimer County: LaPorte, June, 1895, *J. H. Cowen 149* (G, NY); Ft. Collins, *W. F. Marshall 734* (CAC, RM, US); Fort Collins, June, 1898, *C. S. Crandall* (RM); Fort Collins, June 1915, *J. H. Cowen 113* (US), same, June, 1893 (G). Lincoln County: Hugo, July, 1905, *C. D. Marsh* (US). Ouray County: Ridgeway, Aug., 1894, *F. Tweedy 240* (US); Uray [Ouray], May, 1900, *J. E. Payne* (CAC). Prowers County: Lamar, May, 1892, *C. S. Crandall* (CAC). Pueblo County: Pueblo, June, 1891, *E. Penard* (T): Pueblo, June, 1897, collector not given (CAC); Pueblo mesas, May, 1900, *P. A. Rydberg & F. V. Vreeland 5941* (NY, RM). Weld County: Crow Creek, June, 1896, *F. H. Knowlton 97* (NY, US); New Windsor, June, 1895 and 1901, *G. E. Osterhout* (NY); same locality, June, 1905, *G. E. Osterhout* (G, RM). County not given: June, 1970, *E. L. Greene 67* (G); June, 1890, *C. H. Hall* (B).

NORTH DAKOTA. Barnes County: Valley City, Cheyenne Valley, July, 1903, *M. A. Barber 176* (G). Billings County: Marmarth, July, 1909, *V. Bailey 10* (US). Morton County: Parkin, June, 1916, *V. Bailey* (US). County not given: Bad Lands, July, 1891, *H. L. Bolley 132* (RM).

SOUTH DAKOTA. Fall River County: without definite locality, Aug., 1911, *S. S. Visher 2703* (RM); Fall River Falls, June, 1892,

P. A. Rydberg 599 (US). Harling County: Steppe, July, 1910, *S. S. Visher 231* (RM). Meade County: Smithville, June, 1894, *V. Bailey 10* (US). Perkins County: Bixby, July, 1912, *S. S. Visher 615* (RM). Washington County: Sheep Mountain and sand hills south, July, 1911, *S. S. Visher 2406* (NY). County not given: near White Earth River, Missouri, *J. N. Nicolet 161* (G); north edge of sand bluff, *S. A. Skinner 177* (RM).

NEBRASKA. Brown County: Longpine, June, 1897, *J. M. Bates* (RM). Cherry County: Valentine, June, 1891, *J. M. Bates* (G, T). Frontier County: near Curtis, June, 1891, *P. A. Rydberg 46* (NY). Keith County: without definite locality, June, 1890, *G. D. Swezey* (T). Dawes County: Crawford, June, 1891, *J. M. Bates* (B).

KANSAS. Finney County: Garden City, May, 1891, *H. W. Menke* (T). Graham County: without definite locality, June, 1897, *A. S. Hitchcock 81a* (G, NY, RM, US). Logan County: without definite locality, May, 1895, *A. S. Hitchcock 81* (G, NY, RM, US). County not given: western Kansas, 1885, *E. N. Plank 25* (G).

NEW MEXICO. San Juan County: Aztec, May, 1899, *C. F. Baker 435* (G, NY, RM,* US). Dona Ana County: near Organ Mountains, Apr., 1852, *Mexican Boundary Survey 287* (NY, two sheets); opposite Frontera, March, 1852, *C. Wright 1362* (US 20950–1). Without locality: *Mex. Boundary Survey* (US 20941, upper and left-hand specimens); 1851, *C. Wright 1362c* (G); May, 1901, *F. K. Vreeland 821* (NY).

ARIZONA. Pima County: Tucson, March, 1852, *C. C. Parry* (T). Without locality: 1869, *E. Palmer* (US 20944, two upper specimens).

12b. **Lupinus pusillus intermontanus** (Heller) comb. nov. [FIG. 52.]

Lupinus intermontanus Heller, Muhlenbergia 8: 87. 1912.

* The "RM" sheet of this collection has Baker's number given as "433," and is labelled *L. aduncus* Greene, whence Heller has annotated this sheet as follows: "Apparently immature *L. rubens* Rydb. Baker has mixed labels. *L. aduncus* is a perennial. I have the real thing here now, also under 433." It is evidently a part of Baker's collection 435, which seems to have been originally determined as *L. arizonicus*. I may be wrong in assigning it to *L. pusillus* instead of to *L. rubens*. Matured plants with pods and seeds are needed for additional study.

Plants usually more congested than in the species; flowers appreciably smaller, 7–9 mm. long; pedicels and calyx-cup glabrous or sub-villous, lips villous, lower lip less than twice as long as broad, 3–4 mm. long, entire or three-toothed at apex; banner 7–8 mm. long, 5–6 mm. wide, wings about 3 × 6 mm., keel 6 mm. long, straight or the acumen slightly upturned.

CALIFORNIA. Modoc County: Surprise Valley, May, 1879, *J. G. Lemmon* (G). Inyo County: Deep Spring Valley, 1898, *C. A. Purpus 5807* (UC, US).

NEVADA. Clark County: Jean, May, 1915, *K. Brandegee* (UC). Esmeralda County: Candelaria, *W. H. Shockley 270* (UC). Humboldt County: Unionville, June, 1868, *S. Watson 221* in part (US). Ormsby County: Carson City 1864, *C. L. Anderson 84*

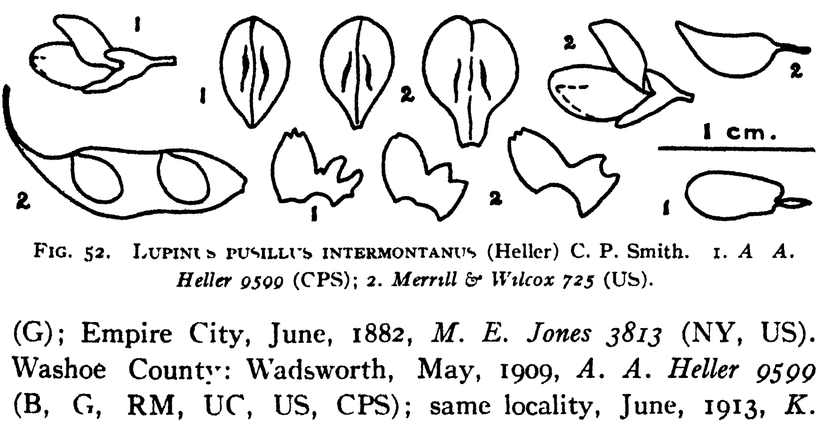


FIG. 52. LUPINUS PUSILLUS INTERMONTANUS (Heller) C. P. Smith. 1. *A. A. Heller 9599* (CPS); 2. *Merrill & Wilcox 725* (US).

(G); Empire City, June, 1882, *M. E. Jones 3813* (NY, US). Washoe County: Wadsworth, May, 1909, *A. A. Heller 9599* (B, G, RM, UC, US, CPS); same locality, June, 1913, *K. Brandegee* (UC).

OREGON. Harney County: Alvord Desert, June, 1896, *J. B. Leiberg 2432* (US); same locality, July, 1898, *W. C. Cusick 2020* (G, RM, UC, US). Lake County: Drews Valley, July, 1893, *Mrs. R. M. Austin* (UC).

WASHINGTON. Franklin County: Pasco, June, 1892, *L. F. Henderson 2362* (G); same locality, May, 1899, *C. V. Piper 2982* (G. NY). Walla Walla County: Wallula, May, 1883, *T. S. Brandegee 706* (G); same locality, May, 1896, *T. Howell 1920* (NY); same locality, May, 1903, *J. S. Cotton 1028* (US); Walla Walla, *Capt. Wilkes 955* (US 21026, right-hand specimen only*); same locality, May, 1903, *J. S. Cotton 1028* (G); plains of the Columbia River,

* The left-hand specimen is *L. subvexus fluviatilis*, in fruit.

1826 *ex Herb. Benth.* (G). Yakima County: Yakima River near Morgan's Ferry, June, 1884, *W. N. Suksdorf 269* (G); west of Mabton, June, 1903, *J. S. Cotton 1115* (US).

IDAHO. Owyhee County: Murphy, July, 1911, *Nelson & McBride 1030* (RM). Twin Falls County: Twin & Shoshone Falls, July, 1911, *Nelson & McBride 1333* (RM).

WYOMING. Big Horn County: Greybull, May, 1910, *M. Cary 521* (US). ? Sweet Water County: thirty-five miles north of Point of Rocks, June, 1901, *E. D. Merrill & E. N. Wilcox 611* (G, US); near Washington Ranch, June, 1901, *Merrill & Wilcox 725* (G, RM, US).

UTAH. Weber County: Ogden, 1872, *Hayden Survey* (US). Beaver County: Frisco, June, 1880, *M. E. Jones* (US). Kane County: Kanab, May, 1894, *M. E. Jones 5286f* (NY, UC, US); twenty miles south of Pahria, May, 1894, *M. E. Jones 5292c* (US).

ARIZONA. Coconino County: Moqui, May, 1869, *E. Palmer* (G).

COLORADO. Huerfano County: Walsenburg, July., 1896, *C. L. Shear 4753, 4800* (NY).

It is interesting to note that this small-flowered variety is almost entirely confined to the Pacific and Great Basin drainage.

Grass rusts of unusual structure*

J. C. Arthur and E. B. Mains

(with two text figures)

The leaves of species of *Olyra* belonging to the tribe Paniceae and of species of bamboos are frequently much alike in form and physical characters, although systematists place the genera nearly at the extremes of the grass series. The resemblances are often so great that only an experienced agrostologist can feel sure of their identity when not accompanied by inflorescence. It is not surprising, therefore, that the rusts on these genera, as well as their hosts, should have been confused. Thus *Uredo Olyrae* P. Henn., described in 1904, to which true *Olyra* rusts have been referred, has recently been found to be on some species of the bamboo genus *Arundinaria*, and *Uredo ignava* Arth. on the genus *Bambos* has only recently been separated from material formerly placed with paniceous rusts.

Not only is there a curious resemblance between the leaves of these two groups of hosts, but also an equally interesting resemblance between some of the rusts that inhabit them. This was first noticed in the uredinia having delicate incurved paraphyses and spores that are more or less thin-walled and colorless. Later it was found that the presence or absence of these weakly differentiated paraphyses is not by itself an important diagnostic character, as the forms called *Uredo paspalicola* without paraphyses and *U. Stevensiana* with paraphyses have been shown to be only extremes of one species having all degrees of intergradation.

In the study of this sort of rusts it became more and more necessary to use a razor and make sections of the sori in order to be surer of their structure. In this manner the paniceous species, *Puccinia tubulosa*, *P. inclita*, and *P. imposita*, were segregated and gradually circumscribed from what had been lumped as *P. sub-*

* Reprints may be obtained by application to the Botanical Department, Purdue University Agricultural Experiment Station, Lafayette, Indiana, under whose auspices the studies here reported were carried out.

striata. Then the telia were found in *P. Chaseana* on a host belonging to a family preceding the Paniceae. The final triumph came in the discovery of telia with the much-studied form, *Uredo pallida* (*Puccinia pallescens*) on *Tripsacum*, a grass belonging to the tribe Maydeae. These telia would doubtless not have been discovered through the usual method of examination by scraping the spores from the leaf with a scalpel. Sections show the sori to be small, indehiscent, and filled with pale, compacted spores (FIG. 2*A*) that are thin-walled and practically without pedicels. Many of the teliospores are three-celled, especially toward the center of the sorus. The whole appearance of the telia and teliospores is quite unlike that of the ordinary grass rusts, and reminds one of those in the group of melampsoraceous rusts represented by *Phakopsora*.

Even with this experience the telia of still another species of rust on *Olyra latifolia* were passed over for a time. The uredinia had been referred to *Puccinia deformata* Berk. & Curt., on the same host, a species with prominent telia, known for over fifty years, but with no described uredinia.* Thin-walled, nearly colorless urediniospores, surrounded by incurved paraphyses, were found, and on the same leaves were discovered telia by the sectioning method. So unusual was the appearance of these telia, however, that they were tentatively referred to the genus *Phaksopsora*, and might have remained there longer had the grasses been known to harbor species of this genus. It was then thought there might have been an error in determination of the host, and that it was a bamboo, instead of the *Olyra*. After much study the following description of a new species of rust was evolved, and incidentally the true urediniospores of *P. deformata* were found.

Puccinia phakopsoroides sp. nov.

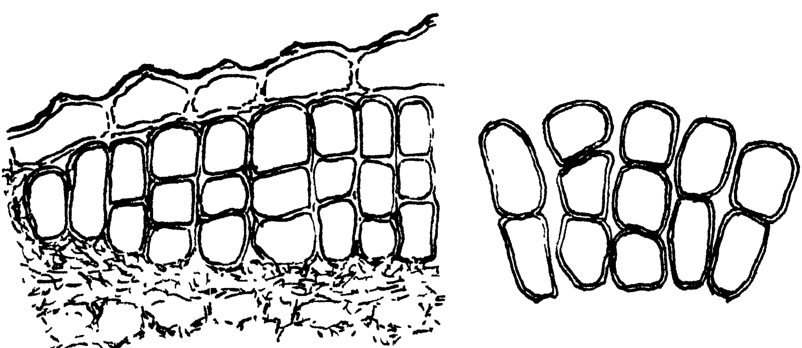
II. Uredina amphigenous, small, round, cinnamon-brown, early naked, ruptured epidermis inconspicuous; paraphyses peripheral, incurved, clavate, 10–12 by 35–50 μ, the wall cinnamon-brown, 1 μ thick, usually thickened up to 2–3 μ on the convex side; urediniospores ellipsoid or broadly obovoid, 19–26 by 27–35 μ; wall slightly brownish or nearly colorless, 1–1.5 μ thick, closely

* See Arthur & Johnston, Uredinales of Cuba. Mem Torrey Club 17: 136. 1918.

echinulate, the pores very indistinct, probably 2 and equatorial.

III. Telia hypophyllous, scattered, squarish-oblong, 0.5–1 mm. long, covered by the epidermis, compact with the spores adhering laterally, brownish-black due to discolored host-tissue; teliospores 1-, 2- or 3-celled, short-cylindric, 8–14 by 24–39 µ, rounded or depressed above and below, somewhat constricted at septa; wall pale-brown or colorless, smooth, thin, uniformly 1 µ or less in thickness, but with an outer colorless layer swelling in in water to 2–3 µ above, demonstrable by staining; pedicel wanting or extremely short and colorless.

On *Olyra latifolia* L., Mayagüez, Porto Rico, January 30, 1890, II, III, *A. A. Heller 4443*, communicated by P. L. Ricker; San German, Porto Rico, December 12, 1913, II, *F. L. Stevens 5849, 5855;* Manati, Porto Rico, July 2, 1915, II, *F. L. Stevens 7700;* Soledad, Cienfuegos, Cuba, November 7, 1915, ii, *J. R. Johnston 247;* Isle of Pines, Cuba, February 20, 1916, II, *Britton, Britton & Wilson 14648;* Ceballos, Cuba, March 24, 1916, II, *J. R. Johnston 509;* Guantanamo, Cuba, February 7, 1918, II, III, *J. R. Johnston 1028* (TYPE).



B

FIG. 1. *Puccinia phakopsoroides: A*, section showing part of a telial sorus and the adjoining host tissues; *B*, teliospores after treatment with potassic hydrate. × 625 diameters.

There is a marked gradation evident in some tropical rusts, especially the grass rusts as indicated above, toward the production of thin-walled, pale or colorless spores. In the uredinia these spores are frequently accompanied with a fringe of incurved, hyphoid paraphyses. In the telia the spores are small and often compacted, long remaining covered by the epidermis. As usual in subepidermal forms, these teliospores have short pedicels.

Puccinia phakopsoroides illustrates an extreme development in this general direction, most strongly seen in the telia. Drawings of the telial sorus of both *P. phakopsoroides* and *P. pallescens* (FIGS. 1*A*, 2*A*) show the spores as cylindrical bodies pressed very closely together, as if restricted by the unyielding epidermis. The spores appear to be less highly differentiated than in most grass rusts, having a variable number of cells with a quite uniform wall, and a pedicel so short and delicate that one is left in doubt whether there is a truly pedicellate cell, or only a hyphal connection with the hymenial layer of the fungus.

Sections of the sorus give a superficial resemblance to forms of *Phakopsora*, especially in the denseness, the pale color and translucency, and in the evenly disposed, vertical rows of apparently similar cells, more cells being in a row at the center of the sorus

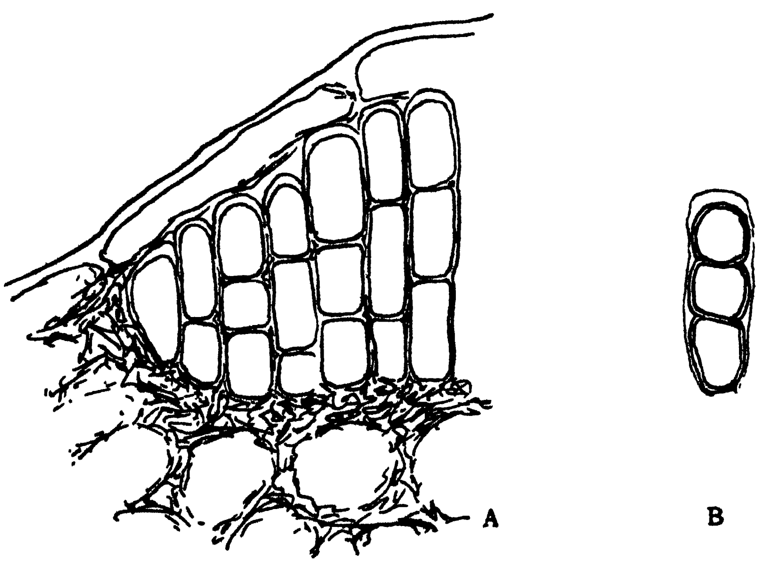


FIG. 2. *A*, section showing part of a telial sorus of *Puccinia pallescens*, with adjoining host tissues; *B*, a teliospore of *P. phakopsoroides* treated with eosin to show the outer hygroscopic layer of the spore-wall. × 625 diameters.

than at the edge. In *Puccinia* each row of cells forms a single spore; in *Phakopsora* there are as many independent spores as there are cells. In *P. phakopsoroides* this resemblance is emphasized when the sections are treated with potassic hydrate, and the spores pressed out of the sorus (FIG. 1*B*). The cells then seem

to separate and appear like one-celled spores in rows, the enveloping outer layer of the spore-wall being invisible, having been swollen and partly dissolved by the potash. However, if sections are stained with eosin, and the spores pressed apart, it is easy to discern a delicate outer layer of wall, swelling in water and becoming thicker above than at the sides of the spore (FIG. 2*B*). The presence of this hygroscopic layer explains why the cells remain in chains, even after macerating in potash, and doubtless why the cells adhere laterally with so much tenacity in an ordinary mount. In *P. pallescens* there is no such hygroscopic layer.

In the above paragraphs comparison has been drawn especially between three tropical rusts of similar but extreme development, which are found on grasses having slight relationship, according to the classification used by modern agrostologists: *Puccinia pallescens* on *Tripsacum*, the first genus in Hitchcock and Chase's "Grasses of the West Indies," *P. phaksopsoroides* on *Olyra*, the fifty-second genus in the same work and *Uredo ignava* on *Bambos*, the one hundred and tenth and last genus of that work. The telia of the last species have not yet been found, but it is confidently believed that when discovered they will resemble those of the other two species named.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1917-1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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BULLETIN

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TORREY BOTANICAL CLUB

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The ferns and flowering plants of Nantucket—XX

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CONCLUSION

The plants of Nantucket enumerated in the catalogue, brought to a close with these pages, number 1,136, including thirty-three natural hybrids. Other probable hybrids and some sixty varieties, mainly such as have received names, have been referred to in the text. Some of these plants that are listed under binomial names are without general botanical consent to be taken as completed species. These, however, are all plants of marked attributes and, however opinions may differ as to the precise status of this one or that, in each case a binomial name has been allowed its sufficient claim unmistakably to denote the plant referred to. This dissembles nothing and has seemed to avoid whatever of factitious precision may inhere in a needlessly composite name. On the other hand forms that pass current under varietal names that seem unduly to honor certain of those variations which, in undefinable number, are common to plants in general, have had only their passing word.

Omitting the hybrids the number of plants formally listed is 1,103.* Of these 746 are native to the island and 362 are introduced.

* This number includes a few mere varieties admitted in the earlier parts of this series, and allows for two species that should be omitted and four here to be added. The eliminations are *Panicum linearifolium* (see Supplementory Notes, *antea*) and *Bartonia iodandra*. The Nantucket plant discussed under this latter name should be referred to *B. paniculata*—a contracted form in which the anthers

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Included among the introduced plants are some thirty species common in cultivation which, although not to be taken as established, have been found persisting in a wild state. The tendency shown by these plants to stray away from their home gardens may well thus be put on record. Should any of them in time come to take a wider place in the flora the beginning of their history as wild plants would become a matter of interest.

Nearly one half of the introduced species are well naturalized and more than two-thirds of these are widespread, including in their number many of the island's abundant plants. About seventy-five species may be accounted common, forty as frequent, seventy as of occasional occurrence.

Almost everywhere where introduced plants abound a much larger proportion of their species than those of the native plants are confined to a single station or to a very few places, and this is notably the case on Nantucket, notwithstanding that an unusual number of native plants are there thus localized. One hundred and seventy of Nantucket's introduced plants have been found at not more than two or three localities, eighty of them at a single station only.

The town of Nantucket itself with its old gardens, its resting wharves, its streetsides and habitable places for plants that have had a quiet past, has come into a flora very interestingly its own,

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are sometimes deep purple, a character hitherto regarded as diagnostic of *B. iodandra*. Some examples, as already intimated, seem to pass into more typical forms of *B. paniculata*, and appear to be similar to the Massachusetts plant reported and figured as *B. iodandra* by Williams (Rhodora 2: 55–57. *pl. 15, f. 5.* 1900), now regarded, I understand, as *B. paniculata*. Professor Robinson who, with Professor Fernald, has recently examined my Nantucket specimens advises me that they are not *B. ioandra*, and specimens of the latter from Newfoundland which were kindly sent to me, show a plant very unlike anything I have met with on Nantucket and beyond question, as I now see it, a strikingly distinct species.

I am indebted to Miss Albertson for specimens of the four additions to the list, one native and three introduced species, as follows:

STEIRONEMA LANCEOLATUM (Walt.) A. Gray. Monomoy, August 22, 1918, in full flower. Collected by Mr. Merriman.

HELIANTHUS MAXIMILIANI Schrad. Field in Madequet, August 15, 1919. Collected in full flower by Miss Ober.

CENTAUREA JACEA L. Field near Franklin Fountain, August, 1915, and July, 1918.

CENTAUREA MACULOSA Lam. Near Big Mioxes, August 23, 1919. Collected in full flower by Miss Milne.

many of whose plants would be looked for in vain elsewhere on the island. So it is that more than one hundred introduced plants have been reported only from the general district of the town. Additions to this domesticated flora now follow on almost from year to year. Freshly seeded lawns and modern gardens add their new comers, and suburban fields where rubbish has been cast encourage the growth of adventitious plants that take their foothold either transiently or tenaciously as time shall prove.

Among introduced species not everywhere found that are well established in the town flora but are rarely if at all seen elsewhere on the island are the following:

Puccinellia distans	*Viola laetecaerulea*
Bromus sterilis	*Aethusa Cynapium*
Carex hirta	*Marrubium vulgare*
Iris pseudacorus	*Physalodes Physalodes*
Lychnis dioica	*Solanum peregrinum*
Chelidonium majus	*Tragopogon pratense*
Geranium pusillum	*Sonchus arvensis*

Some rather unusual alien plants have made their appearance within recent years in different parts of the island about abandoned spots where poultry has been kept, their source of introduction doubtless being the prepared chicken feed now in general use. The mixed growth of weeds that throng such places have yielded the following species, very few of which have been found elsewhere:

Vaccaria Vaccaria	*Conringia orientalis*
Lepidium neglectum	*Lappula Lappula*
Thlaspi arvense	*Amsinckia arenaria*
Neslia paniculata	*Lithospermum arvense*
Erysimum cheiranthoides	*Centaurea melitensis*

In addition to those abundant naturalized plants that everywhere enrich our flora Nantucket has adopted into its vegetation some less usual species that now, common and wide-spread, assert themselves as characteristic island plants. The following may especially be named:

Alopecurus pratensis	*Festuca myuros*
" *geniculatus*	" *capillata*

Aira caryophyllea	*Trifolium dubium*
Carex muricata	*Epilobium hirsutum*
Salix Smithiana	*Centaurium spicatum*
Cerastium semidecandrum	*Apargia autumnalis*
Ranunculus repens	*Artemisia Stelleriana*
Cytisus scoparius	*Arctium tomentosum*

The great majority of the introduced species are herbaceous plants of dry and open ground, many of them succeeding in poor and sandy soils. Less than twenty species are plants of moist or wet places and only one is conditioned by saline influences. Eighteen herbaceous species are twining or climbing plants, three species are woody vines and twelve are shrubs. The introduced trees number thirty-two, although only one has become a strong structural element in the flora, this being our native pitch pine which, history tells us, was first planted on Nantucket in the year 1847. Few other introduced trees have made much response to the conditions that Nantucket has offered, although the cockspur thorn is making itself at home there, and the apple, the pear and the hybrid willow (*Salix Smithiana*) are sparingly more or less widespread. The Scotch pine and the European larch have long formed an extensive and increasing growth at the locality where they were originally set out, and at a few places the locust and the silver poplar are well established, but most of the other trees are not much to be considered, and some number only a few examples that have appeared spontaneously and grown up in out-of-the-way places.

At different times in the past collections of trees were brought to Nantucket and set out in certain places which now, long neglected and apart from cared for land, appear like wild tracts covered with their native growth. Both European and American species were used in these plantings and many of them survive, although few have made much growth. Most of these trees have been noted in the text.

Not many of the introduced plants are from elsewhere than Europe and Eurasia, these numbering some two hundred and seventy-five species. Twelve species belong to Asia and nine are tropical American. Japan, China, India, New Zealand and Mexico have each contributed a single species which is, however, either

a scarce weed or a casual estray from cultivation. Included among the introduced plants are also some sixty North American species, all of which are quite certainly not of the island's indigenous flora.

The families represented by all these plants number sixty-three, eleven being foreign to the indigenous Nantucket flora. As many as nineteen have only a single member and the same number not more than two or three. The most numerous family is the Gramineae with fifty or more members, a number subject to considerable increase by taking account of all named varieties. Among the grasses, as in other groups, the absence will be remarked of some species that might well be looked for. As an instance, so common a port and streetside immigrant as *Eleusine indica* has not yet made its way to Nantucket where, it might be thought, the shipping activities of earlier days might long ago have brought it in.

The family most noteworthy in respect of greater representation by alien than by native members is the Cruciferae with thirty-four introduced species and only four that are native. A less marked preponderance of immigrant species is found in the Caryophyllaceae and Fabaceae, these families having respectively ninteeen and twenty-five alien members against eight and eighteen, in corresponding order, that are indigenous. The number of introduced species belonging to other well-represented families are as follows: Compositae, 28; Labiatae, 18; Cichoriaceae, 11; Scrophulariaceae, 10; Salicaceae, 10; Solanaceae, 9; Polygonaceae, 9; Chenopodiaceae, 8, and Rosaceae, Ammiaceae and Borraginaceae, 7 each. The largest of the native plant families, the Cyperaceae, numbering eighty-seven species, has only two species that are introduced, both *Carices*, and the third largest native family, the Compositae, to which so many of our immigrant weeds belong, numbers but thirty-two introduced species against seventy-two that are indigenous. The Rosaceae and Polygonaceae also preponderate as native families, possessing respectively twenty-nine and twenty indigenous members and only seven and nine that have come by immigration. Of important native families the Juncaceae and Orchidaceae are, as would be expected, totally unrepresented in the introduced flora, and there is only a single in-

troduced fern, the common polypody, this having somehow found lodgment on the island at a single station.

Among the introduced plants yellow flowers and white flowers greatly predominate, their ratios to the total number being respectively over 31 per cent and 28 per cent. White flowers and yellow flowers likewise predominate in the indigenous flora, but here white-flowered plants are relatively, as absolutely, much more numerous, their corresponding ratio being 39 per cent, that of the yellow-flowered 22 per cent. Next in order among the introduced plants come pink-flowered species, including purple-pinks, 19 per cent; purple and blue-purple, 12 per cent; blue, over 6 per cent. Orange and red are each found in only four species, and green-petaled flowers are no less rare. Eliminating those introduced species that seem to have little chance of permanency the resulting percentages show not much change beyond about 4 per cent decrease in the purple- and blue-flowered species and a corresponding increase in the white-flowered.

As among the introduced plants, so in the native flora flowers of some shade of pink, including those scarcely assignable shades lying between pink and purple, are next most numerous after whites and yellows, making up nearly 17 per cent of the whole. Purple and blue-purple follow with over 8 per cent; blue with nearly 4 per cent; red and orange, the one something over, the other a little under 1 per cent. A wide percentage disparity is found between the native and the introduced plants that bear flowers fairly to be described as green, these numbering less than 1 per cent of the introduced species and over 8 per cent of those of the native flora.

From the nature of the case all these percentages are somewhat approximate, not being susceptible of very exact rendering. Petalous flowers only have been taken into the reckoning.

* * * * *

The indigenous flora of Nantucket has its most interesting side to the botanist in its many species of plants that more especially abound southward on the coastal plain. This is its dominating note. But mixing with these plants of southward range are others which trace through the flora a strain of northward relationship that is all the more sharply defined by the emphasis of contrast.

In its more local aspect two interesting features of the flora that will not long escape the exploring botanist are the large proportion of its plants that are confined to the eastern side of the island and the number of species throughout that are strictly localized.

The eastern side of the island is the more diversified in its topography and natural features, abounding in knolls and hollows, in damp open grounds and straggling swamps beset with crowded shrubbery, and hillsides and banks with their herbage and woody growth descending to numerous small ponds and mossy or peaty bogs. It has also more varied and mature tree growths than are found on the western side and reveals better evidences of former forestation. Accompanying these conditions are more varied and richer soils with their responding plant life, and many of the more southern and more northern plants that belong to the flora have their place only here. Here, too, surviving in the thickets and tree groupings, are little colonies of woodland plants, vestiges, we may suppose, of an earlier flora that had its day in that unrecorded period before the woodlands were destroyed.

Extensive dry plains clothed with low herbaceous vegetation spread over much of the southern side of the island, invaded towards the east by barrens of scrub oak and midway in the island by open formations of young pitch pines advancing from denser growths that earlier made their conquest. Westward towards Hummock Pond are veritable tracts of pine barrens which, however, as a modern feature of the island's vegetation, have merely adopted their plants from the general plains flora, not contributing any distinctive species of their own.* Certain reaches of these plains of darker soil call to mind the Hempstead Plains of Long Island. Like the Hempstead Plains, too, these Nantucket plains have their widely distributed assemblage of particular plants, very few of which do not belong as well to neighboring territory.

* It should be noted that among the Nantucket pines are found a few woodland plants that either do not occur at all elsewhere on the island or are nowhere else at home. It would seem to follow that the advent of these plants, or some of them, must have been subsequent to the introduction of the pines. Four of them that have been reported from only one or two localities are *Polypodium vulgare, Corallorrhiza maculata, Linnaea americana*, and *Hypopitys americana*; three others, that are sparingly scattered, are *Hypopitys lanuginosa, Pyrola chlorantha* and *Chimaphila maculata*.

And with few exceptions their characteristic plants are also plants of the Hempstead Plains.*

Among the more interesting are the following:

Schizachyrium scoparium	*Helianthemum propinquum*
Panicum depauperatum	" *majus*
" *meridionale*	†*Hudsonia ericoides*
Aristida purpurascens	*Lechea maritima*
Agrostis antecedens	*Viola pedata*
Carex pennsylvanica	†*Epigaea repens*
" *tonsa*	†*Arctostaphylos Uva-ursi*
Juncus Greenei	*Asclepias amplexicaulis*
Salix tristis	*Agalinis acuta*
Aletris farinosa	†*Houstonia coerulea*
Sisyrinchium arenicola	*Nabalus serpentarius*
Baptisia tinctoria	*Chrysopsis falcata*
Cracca virginiana	*Solidago memoralis*
Lespedeza Bicknellii	*Euthamia tenuifolia*
Linum intercursum	*Sericocarpus linifolius*
Polygala polygama	*Ionactis linariifolius*
Sarothra gentianoides	*Aster concolor*
Helianthemum dumosum	" *dumosus*

Only four of these plants, those marked with a dagger, appear to be wanting on the Hempstead Plains, although the arbutus and the bearberry occur at outlying points. The *Houstonia*, an abundant Nantucket plant, is apparently unknown on Long Island and the *Hudsonia* is a rare plant there.

* * * * *

Over one half of Nantucket's native plants may fairly be accounted as prevailingly more southern in their general distribution. More than one hundred of these reach their northern or eastern limits in Massachusetts, mainly in the Cape Cod region and in the southeastern quarter of the state, and a considerable number of others that pass beyond Massachusetts are reported from no further than southwestern Maine or are of only casual occurrence at more northern or eastern points. Altogether about

* For a very full discussion of the Hempstead Plains and their vegatation, see Harper, The Vegetation of the Hempstead Plains. Mem. Torrey Club 17: 262–286. *pl.* 7. June, 1918.

one hundred and fifty of these plants extend their northeastern limits, in many cases only locally, into Vermont, New Hampshire or Maine, and over seventy others, some of them unknown in Maine, occur as far to the east as the Canadian Maritime Provinces. A smaller group, very noteworthy in its isolation, are found at the extreme eastern extension of the continent in Newfoundland.*

The following plants of Nantucket do not appear to have been reported from any more northern or eastern point, and a considerable number of others have only within recent years been added to the known flora of the eastern Massachusetts mainland. The names used follow those of the catalogue, although some changes have since been adopted.

Lycopodium alopecuroides
Naias guadalupensis
Schizachyrium villosissimum
" *littorale*
Panicum virgatum cubense
" *Bicknellii*
" *albemarlense*
" *auburnae*
Chaetochloa versicolor
Agrostis elata
Elymus halophilus
Eleocharis tricostata
Scirpus Eriophorum
Rynchospora Torreyana†
Carex debilis
" *incomperta*
Arisaema pusillum
Juncus dichotomus
" *aristulatus*
Quercus pagodaefolia
Boehmeria scabra
Polygonum pennsylvanicum var. *nesophilum*
Persicaria setacea
Amaranthus pumilus
Cardamine arenicola
Rubus flagellaris
Aronia arbutifolia
Ascyrum hypericoides
Lechea Leggettii
Opuntia
Vaccinium atlanticum
" *vicinum*
Apocynum pubescens
Setiscapella subulata
Viburnum venosum
Solidago aestivalis
Euthamia minor
Doellingeria humilus

The similarity of the Nantucket flora to that of southern New

* See, especially, Fernald, A botanical expedition to Newfoundland and southern Labrador (Rhodora 13: 109–162 *pl. 86–91.* 1911), a paper of absorbing narrative interest apart from its botanical importance.

† One other New England station for this species is known at East Washington, New Hampshire.

Jersey, which has often been remarked, is strikingly brought out by a mere accounting of the number of coastwise plants common to the two regions. More than one hundred and ninety Nantucket plants belonging to the more southern element of the flora occur in the New Jersey Pine Barrens, and over three hundred are plants of the Coastal Plain elsewhere in that state; while all the maritime plants of Nantucket of general southward range, about forty species, are also of the New Jersey flora.*

Over one half of Nantucket's native plants may be classed as common, about one hundred and forty as frequent and about fifty as of occasional occurrence. As many as one hundred and eighty-two have been found at not more than one to three places and, as far as known, nearly ninety of these occur at only a single station, these categories of rarest plants constituting almost one quarter of the native flora. Nearly three-quarters of these have been found only on the eastern side of the island. The total number of species that are thus restricted number one hundred and seventy-five, and forty-five others are mainly of the same local distribution, these together making up nearly 30 per cent of the flora. Not more than thirty-seven species, or 5 per cent of the flora, are found exclusively on the western side of the island.

Nearly 45 per cent of Nantucket's native plants, about three hundred and thirty species, are plants of low grounds, swamps and pond shores, while little more than one quarter are species that thrive best in dry open ground. Less than twenty species are plants primarily of low or wet woods. Other woodland plants number about ninety species, here for the most part keeping to copses and thickets but also, many of them, appearing on the plains and commons, some having very successfully adapted themselves to these unaccustomed dwelling places. Fogs and moisture from the sea from whatever direction the wind may blow must have had an influence in this, and a curious contributing cause may be seen in the habit of growth of one of the plants themselves that belong to these exposed tracts, the abounding bearberry, whose shining evergreen carpet lies broadspread on hill

* See Stone, The Plants of southern New Jersey with especial reference to the flora of the Pine Barrens and the geographic distribution of the species. Rep. New Jersey State Mus., 1910. The statistics above given have been made possible only through consultation of this work.

and plain. This gives winter protection to the soil and in summer a continuous shade and coolness under its low covering for such woodland plants as here and there may find space enough to make their growth.

Nantucket has been called a treeless island and, apart from the town and the scattered farms, the casual tourist might believe this to be true except for the naturalized pines which are now widely in the landscape. Nevertheless, twenty-five to thirty kinds of trees are native to the island, the larger reckoning allowing for those that, shrub-like on Nantucket, are trees in their full growth. In general, however, the Nantucket trees are not prominent in the vegetation, not many rising above a very moderate height, although there are copses and groupings in low grounds where they attain a good woodland size, and in the seclusion of dense thickets is to be found here and there a beech or an oak little noticeable for height but of a girth of trunk that reports a venerable age. Shrubs abound, and in swamps and low grounds are massed into thickets of the most dense and impenetrable character. The number of species that are botanically shrubs is seventy-two, many of them, however, bearing little distinction of aspect from the herbaceous vegetation amid which they grow. There are eight woody climbing vines and the same number of twining herbaceous species. Of other Nantucket plants having their particular habitats fifty-five belong to the salt marshes and twenty are of the coastal sands. Of thirty-three aquatics three only are exclusively maritime.

The number of native families represented in the Nantucket flora is one hundred and thirteen. Thirty-eight have only one species, twenty-seven two or three species, twenty-six four to nine species and seventeen ten to twenty species. Only four families contain over twenty species, the Rosaceae with twenty-nine and the three predominant families, the Cyperaceae, Gramineae and Compositae with eighty-seven, seventy-eight and seventy-two members. Including in the Rosaceae twenty-four hybrid blackberries that have been described (and other combinations among these occur) its actual membership would approach that of the three highly preponderant families. The ferns number twenty-six, belonging to three families, the Ophioglossaceae, five

species, the Osmundaceae, three species, and the Polypodiaceae, eighteen members, including three commonly regarded as strongly marked varieties and one hybrid.

When discussing the introduced plants it was remarked that they included some sixty North American species that were not indigenous on Nantucket. Some forty of these are common plants of the New England mainland and seventeen are of the west and north. Not more than two or three immigrant native species have come to Nantucket by way of the south, and these seem to be little at home and have not spread from their original stations. Here is perhaps a hint that plants of southern conformities may less readily adapt themselves on Nantucket than do species from the north and west, as if the present climatic conditions of the island might not be encouraging to the advance of more southern types. Should this indeed be true it would seem to reveal that those southern affinities now in such clear aspect in the flora of the island are to be referred back to influences not the same as those of today. And there would be accordance in this with those now well understood evidences of an extensive flora of southern derivation belonging to the New England seaboard of Tertiary time, a flora lost to our later day with these broad coastal tracts that now lie beneath the sea.* Yet not wholly lost. We find it still, much of it, we may believe, in the less disturbed flora of our more southern coastal plain, and we find its remnants persisting as the merest fringe along the withdrawn more northern coast-lines of the present day. And isolated on Nantucket it has been preserved to us in that assemblage of southward ranging plants, now a primary element in the general composition of the flora.

Thus, understanding the far back origin of this relationship, we may the more readily believe that Nantucket's possession of southern plants may be little attributable to influences operative at the present day.

There is other evidence than the general absence of immigrant southern plants on the island that would seem to denote conditions less favorable to more southern than to more northern plants.

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* See Fernald, *loc. cit.* Also, The geographic affinities of the vascular floras of New England, the Maritime Provinces and Newfoundland. Am. Jour. Bot. 5: 219–236. *pl. 12–14.* 1918.

It lies open to the eye on Nantucket that the island is not at all inhospitable to plants of far northern and eastern range, and not a few such species have placed here their outlying southward colonies. And this corresponds in its import to what is true of such of our naturalized plants as have adopted anything like a definite range. Many more Nantucket plants are species whose main colonization in this country is to the northward rather than to the southward. And evidence of like bearing may be seen in this, that many of the island's more southern plants are strictly localized, and, going back, as we may do in certain cases, even to the time of its earliest botanical explorers, have spread not at all from the localities where they were originally found. In the case of coastal plain species an explanation of this is hardly to be sought in soil conditions, and some repressive influence may be suspected in the notably delayed spring on this island and the average low temperature during the growing season that is a feature of its climate.

* * * * *

The northern element in the Nantucket native flora comes to view in its broader aspect in something over one hundred and fifty species that are at least prevailingly more northern in their general distribution. Many of these plants are to be accounted more northern partly in a distributional sense which allows for that equivalency in altitude which has permitted a far southward extension along the Appalachian highlands. Thus while probably less than fifteen Nantucket plants are nowhere found at a more southern point some three times that number are on this island at or near the southern limit of their coastwise range. Other Nantucket northward plants have taken some further way toward the south, a few to be stayed on Long Island, a larger number passing on, not without wide intervals, to find their southern limits in the Pine Barrens and Coastal Plain region of New Jersey. It might be supposed of the maritime species, their way open along the coast as far as had been their bent to follow it, that a freer progress had marked their course. But this has been not at all the case. Some of these plants also have made little or no advance beyond Nantucket, others in like manner with the more inland species have been held at various more southern points.

And it is pertinent here to note that no northward maritime plant of New Jersey is not also a plant of Nantucket, for with the inland species the case is different.

Turning again to Dr. Stone's admirable and enlightening analysis of the flora of southern New Jersey, wherein is much that now enables us better to understand the flora of Nantucket, we find a list of fifty-nine species that range south to New Jersey from the Canadian Maritime Provinces. Forty-one of these plants belong to the Nantucket flora. Of the eighteen that are not found there, ten are also wanting on Long Island and most of the others are all but absent there. And only three of these eighteen plants have been found on Martha's Vineyard. These species are the following:

Lycopodium inundatum	*Carex limosa*
Schizaea pusilla	*Salix lucida*
Scheuchzeria palustris	*Dalibarda repens*
Phalaris arundinacea	*Geum strictum*
Panicularia obtusa	*Hypericum ellipticum*
Scirpus subterminalis	" *Ascyron*
Carex trichocarpa	*Polanisia graveolens*
" *exilis*	*Aster nemoralis*
" *livida*	*Xanthium commune*

It is to be noted of these plants whose course has taken them to southern New Jersey, while withholding them from the related floras of Nantucket, Martha's Vineyard and Long Island, that with few exceptions they are of pronounced general northern range. At their eastern limits they approach the seaboard at a relatively high latitude, most of them ranging westward and bearing south as elevation of land or favoring conditions may allow. Their approach to the New Jersey littoral would thus appear to have been by an inland route by way of the Alleghanian highlands that cross the Hudson and the northwestern part of that state. From their places of abundance to the northeast the drift of their range westward and southward has passed to the north of southeastern Massachusetts and borne them on their highway along the hills whence, at a lower latitude, they have found access to the region of the Coastal Plain. All this the evidence would seem to allow us to believe.

Missing thus certain plants not debarred by climatic conditions Nantucket has received into its flora other northern species even less to be expected there. There is some reason to believe that these plants may not have come to Nantucket directly from the north but from a more eastern part of their range. Just as Nantucket's coastal plain flora partly reappears in the Maritime Provinces and even in Newfoundland, so, conversely, do many northward species characteristically associated in these regions find themselves together on Nantucket. Whether this association of their plants, many of which are of wide distribution, points back to some common heritage in the floras of these regions our present knowledge does not assure us. But something of affinity between these far separated floras seems to sketch itself in outline and not without features more clearly drawn. Such plants of Nantucket as *Fragaria terrae-novae*, *Ribes oxyacanthoides* var. *calcicola* and *Antennaria petaloidea* var. *subcorymbosa* would scarcely be looked for from elsewhere than far to the east. If an ancient land connection has conducted southern forms to these far eastern fields, some counter extension of northern forms, at least in the later age of that one time highway, may well have taken place. It is in point that almost directly to the north of Nantucket in eastern Massachusetts, at no greater distance than Essex County, nowhere of much elevation, many northern plants prevail that have obtained no foothold on Nantucket, even though, as we have seen, the island offers locally soils and conditions that are acceptable to northern woodland plants. And nearer at hand, in the Cape Cod region, where many of the conditions repeat those of Nantucket and many features of the flora are the same, there are, well in place, northern plants that have failed to cross the narrow strip of water to Nantucket. And, emphasizing in an unexpected way this slight rift of disconnection between the similar floras of these coastwise tracts, there are many southern plants of the Cape Cod region, not a few of them well established there, although at the extreme northern limit of their range, that on Nantucket are unknown.*

* See, especially, F. S. Collins, Notes on the Flora of lower Cape Cod. Rhodora 11: 125–133. 1909. Also, Flora of lower Cape Cod; supplementary note. Rhodora 12: 8–10. 1910. Also, Flora of lower Cape Cod; third note. Rhodora 13: 19–22. 1911. Also Sinnott, The pond flora of Cape Cod. Rhodora 14. 25–34. 1912.

If we may picture this region in the formative period of its present flora as enriched with a vegetation crowded along the shore lines of bays and inlets from sound and sea, just as today in such situations plants have assembling places that delight the botanist, then today's surprises in this inward coastal flora have their explanation. For Nantucket, then perhaps little more than a headland flanked with bleak sand wastes along an exposed outer coast, must have proved a difficult and impermanent refuge to many southern species that would find encouragement and perpetuation along the quiet inward shore lines further to the north.

Fragmentary and unclear as these seeming evidences may be they unite in suggesting a closer affinity in Nantucket's flora with the flora of a more eastern region than with that of the northward mainland more nearly at hand. And if there be revealed in this the broken ties of an ancient relationship it traces itself conformably with the general trend of the coast and with that diagonal northeastward-southwestward sweep of distribution that has given their geographic lines to so many of our plants in their eastern range.

The following northward species of Nantucket are unknown in the coastal region of New Jersey, not many of them passing on even to Long Island.

Phegopteris Phegopteris
Isoëtes Tuckermani
Panicularia grandis
Scirpus occidentalis
" *rubrotinctus*
" *pedicellatus*
Eriophorum viride-carinatum
Carex utriculata
" *Goodenovii*
" *monile*
" *subloliacea*
" *prairea*
" *diandra*
Lemna trisulca
Juncus balticus
" *bufonius* var. *halophilus*
Myrica Gale
Corylus rostrata
Persicaria Hartwrightii
Tissa canadensis
Coptis trifolia
Ribes oxyacanthoides var. *calcicola*
Fragaria terrae-novae
Argentina litoralis
Rubus strigosus
" *triflorus*
Lathyrus pilosus
Ilex bronxensis
Epilobium palustre
" *lineare*
" *strictum*

Epilobium adenocaulon
Ligusticum scoticum
Coelopleurum actaeifolium
Chamaepericlymenum canadense
Chiogenes hispidula
Oxycoccus Oxycoccos
Pneumaria maritima
Mentha glabrata
Agalinis paupercula
Galium palustre
Linnaea americana
Antennaria neodioica var. *attenuata*
Antennaria petaloidea var. *subcorymbosa*

* * * * *

A word remains to be said of the degree of completeness with which the flora of Nantucket is now probably known. The botany of many another region of even greater extent might be very thoroughly chronicled from far less investigation than has been bestowed on Nantucket. Here, as we have seen, are found conditions that ask for close work by the explorer and notwithstanding what has already been accomplished the island today remains a broad and an inviting botanical field. I do not in the least doubt that a systematic exploration continued through an entire season would bring to light many unexpected things and add materially to the list of Nantucket plants. Many a bog, or shrubby patch, or little space of open hillside or plain is alone the home of some noteworthy Nantucket species, and the difficult thickets, especially, cannot yet have yielded all their secrets. When we recall how easily, out of their particular season, many plants may miss the eye, and that there is already a long list of Nantucket species, each one having its single spot somewhere in the fifty square miles that make up the island's area, the possibilities of new discoveries may well stir the later explorer with something of the enthusiasm which animated those who were pioneers.

I should suppose that it were well within the possibilities that 10 per cent or more of the native flora remained to be brought to light, and that an addition of not less than 5 per cent to the number of plants already known might be confidently looked for. My own visits to the island have been never for more than brief periods and have wholly missed the important seasons of midsummer in the last weeks of July and of August. Nor have I collected on Nantucket in mid-August since 1904, nor in the autumn since 1907, nor explored there at all since 1912. It may be further

useful to the future explorer to speak of certain parts of the island where, especially, careful work remains to be done. In the southwestern quarter that not extensive tract known as "The Woods" which, although treeless, must at some unrecorded period have justified its name, has probably not been visited in every season, and Trot's swamp and the maze of thickets, wet and dry, in Squam, as well as parts of Polpis, are places which not every collector may have cared to penetrate. At Coskaty there is a thickly wooded tract where it is probable few botanists have ever been. Only once and too hurriedly have I gone amid the thick undergrowth of this piece of timber and its complete exploration has remained an object unattained. Nor has my hope yet been realized of sometime traversing the long sand strip between Coskaty and Great Point.

Reading again the pages of Mrs. Owen's catalogue through its perspective of more than thirty years, we are reminded anew of the singular rarity on Nantucket of many of its most interesting plants, and of their close seclusion in those chosen spots that have given them protection. Some of these plants, many of them, indeed, that were discovered by Mrs. Owen, or announced through her by the active group of collectors which she inspired, have rarely been encountered since. And as many as fifteen or twenty species then reported, which we have no reason to believe are not growing somewhere on Nantucket today, remain to be rediscovered by those whose pleasure it shall be to continue the study of the island's botany so long ago begun.

Sex in the Conjugatae and the relative frequency of the different types of conjugation

H. W. THURSTON, JR.

It has been much disputed in the past whether there is a true sexual differentiation between the cells that fuse in the process of zygospore formation as found in the filamentous Conjugatae. Bessey (2) and others have argued that the process probably is sexual in cases of scalariform conjugation at least. Bennett (1) says: "I do not myself entertain any doubt that even in lateral conjugation there is an incipient differentiation of sex, although this differentiation extends only as far as the individual cells." The Wests (6) have gone even farther, and say, "against the sexuality of the Zygnemeae only two plausible objections can be raised; these are the phenomena of *lateral* and *cross-conjugation*," but they conclude that there is no reason even on these grounds to regard the Zygnemeae as other than sexual. Regarding the Mesocarpeae however, they say further that "indications of sexuality . . . are much less marked than in the Zygnemeae," and, "as these scarcely appreciable indications of sexuality are often absent, we may regard the Mesocarpeae as having lost almost all traces of differentiation into male and female gametes." Still later, G. S. West (7, p. 135) discusses the question as follows: "The term 'sexual' is often used to embrace all forms of gamogenesis, and is in this sense firmly established in botanical literature. It would, however, be more scientifically accurate to distinguish between gamogenesis (or the mere fusion of gametes) and sexual reproduction in the narrower sense (which should be restricted to those cases where there is a fusion of clearly differentiated ♂ and ♀ gametes). From this point of view, therefore, gamogenesis although including sexual reproduction is not identical with it. It must be remarked, however, that the gradation is so fine, especially in the Chlorophyceae, that the distinction is scarcely worth making. Sometimes, as in many of the Zygnemaceae, the gametes are morphologically indistinguishable but physiologically differentiated,

and in these cases there is often a morphological differentiation of the gametangia." The question certainly arises whether we ever find cases of reproduction by cell fusion as contrasted with reproduction by cell division in which the process is not to be considered as involving the essential features at least of sexual reproduction. We have obviously come to think of sexuality as involving some fundamental difference between the cells that fuse or conjugate, and consequently when we can find no visible difference between the gametes and can not in any way tell the male from the female, we find ourselves inclined to doubt the so-called sexual nature of such a conjugation. This is the case for all species of filamentous Conjugatae that form their spores midway between the two conjugating cells (TABLES II and IV) and the common doubt as to the sexual nature of this conjugation is expressed by the above quotation from West. Naturally among low plant forms of this kind we should expect to find the most primitive kind of sexuality in its most fundamental expression. Many of our fundamental ideas regarding the nature of sex processes we owe to the study of these very algal forms. Schmitz in 1879 saw two nuclei in a zygospore of *Spirogyra* "approach each other and fuse to a single nucleus." This was the first description of the nuclear behavior in the sexual process in the plant kingdom and was made before any such process was known to occur in any of the higher plants. It is certainly possible that by the intensive study of these primitive forms we may further clarify our ideas as to the nature and origin of sex.

Wittrock (8) has defined a zygospore as "a spore formed by an act of fecundation in which two or more cells of the same kind, not sexually different, have participated." Can we accept such a definition, and at the same time accept conjugation in these forms as being essentially a fecundating reproduction? If we can, the formation of gametes can involve only the difference between somatic cells as such and gametes, as such, rather than any essential difference between the two gametes themselves. Perhaps, after all, cells fuse rather because they are alike than because of an inherent difference between them. Certainly both of a pair of fusing cells in *Spirogyra* differ in some way from the somatic cells from which they arose. Such differences between

gametes as those of size and motility are perhaps to be considered as mere adaptations introduced in evolution to facilitate the bringing together of the two elements. Tröndle (5), for example, claims to have proved that the vegetative cells of the *Spirogyra* filament are haploid; then the difference, in the case of *Spirogyra* at least, between somatic cells and gametes can not be one of chromosome number, but some difference there must be to inhibit further vegetative division in any given cell of a filament and cause instead a union of that cell with another which has undergone a similar change. The gametic nature of any cell in a filament would then be fixed when it ceases to have the power to divide but instead has a new found power to unite with some one of its fellows. At that moment the cell ceases to be a somatic cell and becomes a gamete.

Cunningham (3) has reviewed the literature of the sexuality of *Spirogyra* rather thoroughly, but he throws out the cytological evidence of Tröndle when he compares the filament of *Spirogyra* with the sporophyte of higher plants. He concludes that "reduction may occur in the zygote, in which case a filament wholly of one sex arises, or reduction may occur just previous to reproduction, in which case . . . . . filaments of a bisexual nature are produced, which would conjugate either laterally or by cross-conjugation." Two of the species described by Tröndle as having the reduction take place in the zygote, would therefore according to Cunningham produce filaments "wholly of one sex," which however are known to conjugate in both the lateral and scalariform manners (see TABLES I and III). These are *S. longata* and *S. neglecta*. The real evidence of fecundation in these forms is not to be found in a visible or measurable difference between the filaments or even between the cells that fuse, nor is it to be found in the method of conjugation, whether lateral, scalariform, or cross conjugation, but it lies in the newly achieved possibility of fusion itself with resultant doubling of the nuclear material and the subsequent reduction division, which as far as the evidence extends at present takes place on the germination of the zygospore. If we believe that similarity between gametes favors rather than hinders fusion, then there is nothing at all startling in considering lateral conjugation as a fertilization even if the cells taking part are sister

cells, and nothing startling in considering the conjugation in all the species of the Mesocarpeae as fecundation. Even a case such as that described by Petit (4) for *S. mirabilis*, where he says that the contents of a single cell separate into two parts which reunite forming a spore, might be considered as a fertilization. There may also be an explanation here for many of the so-called aplanospores and parthenospores, which when the facts are fully known may be found to go through some process similar to that described by Petit for *Spirogyra* or by Woodruff for *Paramoecium*.

My purpose in gathering together the subtended tables has been to show the relative frequency of the different types of conjugation as shown in the literature. It is obvious that lateral conjugation is very common. This fact, together with occasional observations of cross conjugation, and the fact that both lateral and scalariform conjugation are often found not only in the same species, but in one and the same filament, go to prove that the individual cell rather than the filament should be regarded as the unit when the fusions in these forms are being considered. It is of course quite impossible in the present state of our knowledge to estimate finally the validity of many of these species. No claim is made for the completeness of the tables nor that all synonyms have been eliminated. In my opinion, however, they show approximately the proportions in which the different types of conjugation have so far been described in the literature and may be useful to students of the general problems of sex.

The principal sources of the tables are such standard works as Wolle, Hassall, Cooke, Petit, De Toni, West and Collins (as indicated in parentheses), although numerous shorter papers have also been consulted. Acknowledgment is due Dr. R. A. Harper for suggestions leading to the compilation of the tables. Species which do not appear are omitted because no drawing or definite statement as to the method of conjugation could be found in the literature.

TABLE I

CONJUGATION SCALARIFORM, SPORE IN ONE OF THE CELLS

Zygnema affine (Hassall)	*Zygnema cylindricum* (Transeau)
" *anomalum* (Wolle)	" *cruciatum* (Wolle)
" *chalybeospermum* (West)	" *cyanospermum* (Cleve)
" *Collinsianum* (Transeau)	" *ericetorum* (West)

Zygnema insigne (Wolle)
" *leiospermum* (Cooke)
" *peliosporum* (Wittrock)
" *purpureum* (Wolle)
" *rhynchonema* (West)
" *spontaneum* (West)
" *stellinum* (Wolle)
" *Vaucherii* (Cooke)
Spirogyra adnata (Wolle)
" *affinis* (Fritsch)
" *angolensis* (West)
" *arcta* (West)
" *bellis* (Petit)
" *Borgeana* (Transeau)
" *calospora* (Wolle)
" *catenaeformis* (Petit)
" *circumlineata* (Transeau)
" *communis* (Wolle)
" *condensata* (Wolle)
" *crassa* (Wolle)
" *cylindrospora*
" *daedalea* (Transeau)
" *decimina* (Petit)
" *diluta* (Wood)
" *dubia* (Wolle)
" *ellipsospora* (Transeau)
" *Farlowii* (Transeau)
" *flavescens* (Wolle)
" *fluviatilis* (Wolle)
" *fuscoatra* (Wolle)
" *gallica* (Petit)
" *gracilis* (Wolle)
" *Grevilleana* (Petit)
" *Hantzschii* (Wolle)
" *Hassallii* (West)
" *hydrodictya* (Transeau)
" *illinoiensis* (Transeau)
" *inflata* (Cunningham)
Spirogyra insignis (Petit)
" *Juergensii* (Wolle)
" *jugalis* (Cooke)
" *Lagerheimii* (Wittrock)
" *laxa* (Petit)
" *longata* (Fritsch)
" *lutetiana* (Wolle)
" *majuscula* (Wolle)
" *maxima* (West)
" *micropunctata* (Transeau)
" *neglecta* (Petit)
" *nitida* (Cooke)
" *orbicularis* (Cooke)
" *orthospira* (Wolle)
" *parvispora* (Wolle)
" *porticalis* (Cooke)
" *pratensis* (Transeau)
" *protecta* (Transeau)
" *punctata* (Wolle)
" *quadrata* (Petit)
" *quinina* (Cooke)
" *rectangularis* (Transeau)
" *reflexa* (Transeau)
" *rivularis* (Wolle)
" *setiformis* (Wolle)
" *serratum* (Hassall)
" *Spreeiana* (Petit)
" *subaequa* (Wolle)
" *subsalsa* (Wolle)
" *submaxima* (Transeau)
" *tenuissima* (Petit)
" *ternata* (Petit)
" *varians* (Wolle)
" *velata* (West)
" *Weberi* (Petit)
" *Welwitschii* (West)
Plagiospermum tenue (Wolle)
Sirogonium stricta (Wolle)

TABLE II

CONJUGATION SCALARIFORM, SPORE IN THE CONJUGATION TUBE

Zygnema Collinsianum (Transeau)
" *parvulum* (Wolle)
" *pectinatum* (Wolle)
" *Ralfsii* Wolle)
Zygogonium aequale (Wolle)
" *Agardhii* (Wolle)
" *decussatum* (Wolle)
" *ericetorum* (Cooke)
" *gracile* (Cooke)
" *rhynchonema* (West)
" *terrestre* (Wolle)
Mougeotia angolensis (West)
" *Boodlei* (West)
" *calcarea* (Wittrock)
" *capucina* (West)
" *delicatula* (Wolle)
" *divaricata* (Wolle)
" *genuflexa* (Collins)
Mougeotia glyptosperma (Wolle)
" *gracillima* (Wittrock)
" *irregularis* (West)
" *laetevirens* (West)
" *laevis* (Cooke)
" *minnesotensis* (Wolle)
" *numuloides* (Wolle)
" *parvula* (Wolle)
" *pulchella* (Wittrock)
" *quadrata* (West)
" *sphaerocarpa* (Wolle)
" *tenuis* (Wittrock)
" *tumidula* (Transeau)
" *uberosperma* (West)
" *verrucosa* (Wolle)
" *viridis* (Wittrock)
Mesocarpus crassus (Wolle)
" *depressus* (Cooke)

Mesocarpus macrosporus (Wolle)
" *radicans* (Wolle)
" *recurvus* (Wolle)
" *robustus* (Wolle)
" *scalaris* (Wolle)
Debarya africana (West)
" *americana* (Transeau)
" *calospora* (West)
" *decussata* (Transeau)
Debarya desmidioides (West)
" *glyptosperma* (Wittrock)
" *Hardyi* (West)
" *laevis* (West)
" *immersa* (West)
" *reticulata* (West)
Pyxispora mirabilis (West)
Temnogametum heterosporum (West)

TABLE III

CONJUGATION LATERAL, SPORE IN ONE OF THE CELLS

Zygnema insigne (Hassall)
" *leiospermum* (Cooke)
" *stellinum* (Wolle)
Mougeotia nummuloides (West)
" *parvula* (West)
Spirogyra affinis (Fritsch)
" *angulare* (Hassall)
" *bellis* (Cooke)
" *catanaeformis* (Petit)
" *communis* (Petit)
" *condensata* (Cooke)
" *crassa* (Cooke)
" *decimina* (West)
" *dubia* (West)
" *flavescens* (Cooke)
" *gracilis* (West)
" *groenlandica* (West)
Spirogyra Grevilleana (Petit)
" *Hassallii* (Wolle)
" *hydrodictya* (Transeau)
" *inflata* (Cunningham)
" *intermedia* (Hassall)
" *insignis* (Cooke)
" *Juergensii* (West)
" *longata* (Tròndle)
" *mirabilis* (Wolle)
" *neglecta* (Tröndle)
" *pratensis* (Transeau)
" *quadrata* (Cooke)
" *rectangularis* (Transeau)
" *Spreeiana* (Petit)
" *tenuissima* (Petit)
" *varians* (Petit)
" *Weberi* (Cooke)

TABLE IV

CONJUGATION LATERAL, SPORE IN THE CONJUGATION TUBE

Mesocarpus pleurocarpus (Cooke)
Mougeotia genuflexa (West)
Mougeotia mirabilis (Wolle)
Temnogametum heterosporum (West)

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Studies on plant cancers—I. The mechanism of the formation of the leafy crown gall*

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(WITH PLATES 17 AND 18)

Smith in 1916 (1) announced a new type of crown gall, consisting of leafy shoots, which was produced by inoculating the leaf axils of a plant, where a dormant bud was present, with *Bacterium tumefaciens*. Similar leafy crown galls were produced by inoculating the midvein of the leaf of the tobacco, with the bacterial organism. Smith considered this type of crown gall identical with the atypical teratoid embryomata found in the animal. In 1917 (2) he showed further evidence of the power of this organism to produce leafy shoots in fifteen different families of plants. He contends that the leafy tumor is produced by inoculating *Bacterium tumefaciens* into the tissue of a susceptible species in the vicinity of totipotent cells.

Levin and Levine in 1918 (3) indicated that these leafy shoots are always secondary and that the crown gall develops first and then a group of crown gall cells become differentiated and give rise to a tissue, an organ, or potentially an entire plant, the leafy shoot. According to these authors, such differentiation of cells of a malignant tumor does not occur in animal cancer. Crown gall represents only one type in the large group of pathological processes known under the general term "cancer."

It occurred to the writer that if, as Smith claims, *Bacterium tumefaciens* inoculated into the epidermis (epithelium) of a plant gives rise to an epithelioma and a similar inoculation into the cortex or vascular bundles (connective tissue) produces a sarcoma, then the inoculation of a plant in any region of totipotent cells (bud Anlage), which are known to produce leafy shoots under normal conditions should produce them under the added stimulus of *Bacterium tumefaciens* much more readily and in greater abundance.

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It is well known that when *Bryophyllum calycinum* leaves are detached from the mother plant and are put on moist soil the marginal notches of the leaves, at which totipotent cells are found, develop into leafy shoots and eventually form new plants. For this reason, leaves and stems of *B. calycinum* were used to study the effect of the bacterium on the leafy shoot formation.

METHOD AND MATERIAL

The leaves of *B. calycinum* were detached from the plant and were placed on moist soil in pots in the greenhouse. The marginal notches of one side of the leaf, right or left, upper or lower, were inoculated, by pricking the tissue five to ten times with a delicate needle containing a culture of *Bacterium tumefaciens* from five to forty days old. The uninoculated notches of the opposite side of the leaf, served as controls, after they had been pricked with a sterile needle. Entire leaves with each notch pricked five to ten times with a sterile needle were also used as controls. Leaves in all stages of development were used. The veins of leaves and growing regions of stems of the *Bryophyllum* were also inoculated with *Bacterium tumefaciens.* In all over a thousand inoculations were made. It may be stated that thin young leaves did not lend themselves to these experiments, because they dried out too rapidly. It was likewise found that normal embryos develop better in the greenhouse than in the open.

As a rule, two days after inoculation with *Bacterium tumefaciens* both the infected and control notches showed necrotic areas in those regions. It appeared, however, that the wounds infected showed greater areas of dead tissue, which subsequently caused deeper indentations at the margin of the leaf. This was also observed by Levin and Levine (3) for a number of plants. The uninfected or control notches recovered readily and although slight scars were formed, the bud Anlagen in the notches developed into normal embryos forty to seventy days after injury. Inoculations were made: (1) into the notches of *Bryophyllum calycinum* leaves; (2) into the leaf in the vicinity of the notches; (3) into the midveins of the leaf; and (4) into the growing regions of the young stems of this plant.

OBSERVATIONS

1. *Inoculation of Bacterium tumefaciens into the notches of Bryophyllum calycinum leaves*

The study of this material shows that in the great majority of cases, the notches infected with *Bacterium tumefaciens*, instead of causing the development of leafy shoots, formed ordinary crown galls. FIG. 1 represents a young detached leaf forty-five days after having been placed on soil and having had the basal notches inoculated with the bacterium. The apical notches were pricked with a sterile needle and served as controls. The inoculated notches show well-developed ordinary crown galls without leafy shoots, while the control notches on the ventral surface show the beginning of the development of leafy shoots.

FIG. 2 represents an older leaf, in which the basal notches were inoculated forty-five days previously. In this case no galls or shoots have as yet been formed at the notches but the control notches are beginning to proliferate and the uppermost notch of the leaf has produced a shoot. FIGS. 3 and 4 represent the ventral and dorsal surfaces of a detached leaf seventy days after inoculating the basal notches with the bacterium. All the basal, infected notches show well-developed galls without leafy shoots on the ventral surface (FIG. 3). The majority of the control, apical notches have already developed leafy shoots. FIG. 5 represents an old detached leaf grown on soil, 140 days after the basal notches were infected. The mother leaf is seen in the center of the figure with a number of well-developed shoots coming from the apical notches. The basal, inoculated notches all show well-developed crown galls. In one instance a poorly developed shoot, visible in FIG. 5 over the largest gall, made its appearance. A similar condition is shown in FIG. 7. These leafy shoots appeared much later in the development of the gall. This seems to show the dwarfing and inhibiting effect the crown gall organism has on the growth of the bud Anlage.

2. *Inoculation in the vicinity of the notch*

When the inoculation is made near the notch instead of in it, a crown gall is developed alongside of a poorly developed leafy

shoot. This is shown in FIG. 6, which represents a leaf forty-five days after inoculation with *Bacterium tumefaciens.* The control notch developed a much larger and more vigorous leafy shoot.

FIG. 7 represents an old detached leaf, 140 days after inoculation. Here again several of the inoculations were made near the bud Anlagen. To the left are seen the large plants which have developed from the control notches. At the right, in the foreground, are seen three galls; next to the lower ones there appear small dwarfed plants. It appears that the galls have interfered with the normal development of these leafy shoots when compared with the large normal plants seen to the left.

3. *Inoculation in the midvein*

It may be assumed that the midvein may have totipotent cells which by the inoculation of *Bacterium tumefaciens* can be stimulated to develop leafy shoots. Forty leaves of *B. calycinum,* both young and old, detached from and attached to the mother plants, were inoculated with *Bacterium tumefaciens* by means of pricking the midvein of the leaf with a fine needle. All produced crown galls within a month after the inoculation. FIGS. 2 and 3 show the appearance of such galls on young leaves forty days after the inoculations were made. FIG. 8 represents an old leaf attached to the mother plant. A large gall has been formed on the midvein by inoculating it with the bacterium five months previously. The tumor is a charcteristic crown gall consisting of a great number of tubercles. This leaf was carefully guarded in the hopes that these tubercles would produce leafy shoots. FIG. 9 represents the gall shown in FIG. 8, nine months after inoculation. The leaf became detached and withered. The gall has grown considerably larger, taking on a cylindrical shape, and has become covered with numerous tuberosities. No leafy shoots were formed.

4. *Inoculation of the growing region of the stem*

A large number of *B. calycinum* plants were also inoculated with *Bacterium tumefaciens* in the growing region of the stem with the object of stimulating there the possible totipotent cells to leafy shoot formation. FIG. 10 (*a, b, c, e, f*) represents a few of the

young plants in which the growing regions had been inoculated four months previously. In one case only has a small leafy shoot been formed (FIG. 10, *b*). This, however, appeared after the crown gall had been well established. The plants are all dwarfed, as may be seen by comparing FIG. 10, *a*, *b*, *c*, *e*, and *f*, with *d*, one of the control plants.

SUMMARY AND CONCLUSIONS

1. *Bacterium tumefaciens* inoculated by pricks of a delicate needle into the marginal notches of a leaf of *Bryophyllum calycinum*, where totipotent cells are present, results in the formation of a crown gall as readily as in other plants used for inoculation but without leafy shoots.

2. Inoculation of *Bacterium tumefaciens* into the tissue of a leaf of *B. calycinum* in the vicinity of a small bud causes the formation of a gall and interferes with the normal development of the bud or leafy shoot.

3. Inoculation of *Bacterium tumefaciens* into the midvein of a young or old leaf detached from or attached to the mother plant results in the development of a large gall without the development of leafy shoots.

4. Inoculation of *Bacterium tumefaciens* into the growing region of the stem of a young plant causes the development of the ordinary crown gall with the occasional and subsequent development of a leafy shoot.

5. *Bacterium tumefaciens* does not cause the formation of leafy shoots in *Bryophyllum calycinum* but rather inhibits and retards their normal development, when inoculated into the totipotent cells which appear at the notches of the leaf.

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Description of plates 17 and 18

PLATE 17

FIG. 1. Young leaf of *Bryophyllum calycinum*, showing well-developed crown galls at the basal notches, inoculated with *Bacterium tumefaciens* forty-five days previously.

FIG. 2. Older leaf, control notches showing leafy shoots, none appearing at the inoculated notches forty-five days later. The midvein, also inoculated, shows ordinary crown gall.

FIGS. 3, 4. Ventral and dorsal surfaces of a leaf, the basal notches and mid-vein of which were inoculated with *Bacterium tumefaciens*, showing well-developed galls without leafy shoots. The control, apical notches show normal leafy shoots.

FIG. 6. Young leaf, in which the inoculations were made near the apical notches, showing a dwarfed leafy shoot with a crown gall attached to it. One of the control notches shows a well developed leafy shoot.

FIG. 10. Young plants. In *a*, *b*, *c*, *e*, and *f*, the growing regions were inoculated; in *d*, there was no inoculation.

PLATE 18

FIG. 5. Old leaf, inoculated at the basal notches 140 days previously, showing a large crown gall. The control notches show normally developed plants coming from them.

FIG. 7. Old leaf, 140 days after inoculations were made near the notches, showing dwarfed leafy shoots growing in contact with crown galls. The control notches have developed normal plants.

FIG. 8. Old leaf attached to mother plant, showing a large gall on the midvein produced by inoculating it with *Bacterium tumefaciens* five months previously.

FIG. 9. Same leaf now detached, nine months after inoculation.

INDEX TO AMERICAN BOTANICAL LITERATURE

1914–1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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Preliminary notes on the embryology of Reboulia hemisphaerica

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(WITH PLATE 19)

The object of this paper is to present a part of a more extended study on the embryology and cytology of *Reboulia hemisphaerica* (L.) Raddi. Only certain stages in the process of fertilization and in the early development of the embryo sporophyte will be considered at this time. The description of various other stages in the life history together with a summary of the previous literature on *Reboulia* will be left for a subsequent report.

FERTILIZATION

The male gamete in the bryophytes may undergo two series of marked morphological changes. The first series includes the steps leading from the non-motile condition of the androcyte (the cell which directly becomes transformed into the mature sperm) through the formation of the actively motile free-swimming sperm. The second series includes the reverse steps and occurs in those cases where a sperm reaches an egg. In this second case the motile sperm becomes again non-motile with a resting nucleus similar to that of the androcyte or androcyte mother-cell. Details of the main stages in the first series have been carefully described for numerous liverworts and mosses. The processes accomplished in the second series, after the sperm reaches the egg, are not so well known. However, soon after

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reaching the egg the sperm nucleus is found to have the form and structure of a nucleus in the resting stage (FIG. 1). Quite similar conditions have been reported by Black (1) and Garber (3) for *Riccia* and by K. Meyer (4) for *Corsinia*. The form and structure of the egg and sperm nuclei at this stage are to a certain extent similar (FIG. 1). The egg nucleus is larger and shows a coarser and more open disposition of the chromatin. An unstained area surrounds the nucleolus. A smaller nucleolus is present in the sperm nucleus. The latter as a whole stains somewhat more heavily than does the nucleus of the egg.

The accompanying figures are drawn as nearly as possible in that position which is occupied in nature. For instance, the necks of the archegonia at this stage of development project obliquely downward or toward the substratum. Consequently it will be seen that, in FIG. 1, the sperm nucleus lies in contact with that side of the egg nucleus which is toward the neck of the archegonium. The membrane of the egg nucleus is somewhat infolded along the surface of contact.

Compared with corresponding stages in the life history of gymnosperms and angiosperms we know very little concerning the details of nuclear behavior in this and further stages of fertilization.

EARLY DIVISIONS OF THE EMBRYO

The first division wall of the zygote is laid down transversely. FIG. 2 represents the telophase of this first division, with the cell plate in the process of formation. The spindle lies parallel with the longitudinal axis of the venter of the archegonium; consequently a transverse basal wall results (FIGS. 2 and 3). In FIG. 3 the nuclei are in the prophase of subsequent division; "a" represents the hypobasal cell or that one next to the base of the archegonium, and b, the epibasal cell or that one next to the neck of the archegonium. The second division is transverse and occurs in the epibasal cell (compare FIGS. 3, 4, 5 and 6). The epibasal cell (FIG. 3, "b"), with the chromosomes clearly differentiated, is in a more advanced stage of prophase than the hypobasal cell. There is also evidence of centrosomes or centrosome-like structures connected with the nucleus. FIG. 4 represents the second division completed. Later stages (compare FIGS.

3, 4, 5, 6 and 11) indicate that from the hypobasal cell is developed the foot and from the epibasal cell the stalk and sporangium of the mature sporophyte.

A third division follows in either the middle or apical cell of the tier of three (FIG. 4) which results from the first and second divisions. Compare FIG. 5, which shows a tier or series of four cells, with FIG. 4. Then follows (FIG. 6) a division in the basal or foot cell at right angles to the first three division walls. The foot at this stage has become quite dense in protoplasmic contents.

The order of divisions just described seems to represent the usual conditions. Compare, however, FIGS. 2–6 with FIGS. 7–10. In each section represented by FIGS. 7 and 9 there is a triangular-shaped apical cell, while in FIGS. 8 and 10 both apical and basal cells of triangular shape are present. FIG. 11 represents a slightly different condition, in which the foot has become divided into an irregular group of cells.

In no case do we find the same sequence of early divisions as described by Cavers (2). In speaking of the early divisions of the sporophyte of *Reboulia*, he says, "The transverse basal wall is followed by two sets of nearly equal vertical walls which intersect each other at right angles, so that the embryo shows a regular octant stage."

SUMMARY.

The egg and sperm nuclei are both in a resting condition in the earliest stages of fusion.

Among the Bryophytes little is known concerning the details of nuclear behavior during the stages of fertilization.

The earliest divisions of the zygote are transverse. A longitudinal series or tier of four cells may be formed.

Occasionally, however, both apical and foot cells of triangular outline may be formed, or the basal cell may divide into an irregular group which constitutes the foot.

Of the first two cells formed, the hypobasal cell evidently produces the foot, and the epibasal cell the stalk and sporangium of the mature sporophyte.

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Explanation of plate 19

The figures were drawn by Miss Mary C. Blair.

FIG. 1. Early stage of fusion of the egg and sperm nuclei, × 1775.

FIG. 2. Telophase of first division of zygote, × 565.

FIG. 3. First division of zygote completed; hypobasal cell "a," and epibasal cell "b" in prophase of subsequent division, × 735.

FIG. 4. Division of epibasal cell completed, showing tier of three cells, × 565.

FIG. 5. Young embryo consisting of tier of four cells, × 565.

FIG. 6. Hypobasal cell divided longitudinally; cell next above in process of longitudinal division, × 565.

FIG. 7. Young embryo with wedge-shaped apical cell, × 735.

FIG. 8. Young embryo with both basal and apical cells triangular in shape, × 735.

FIG. 9. Embryo, older than in any of the preceding figures, with wedge-shaped apical cell × 565.

FIG. 10. Slightly more advanced embryo than in FIG. 9, showing both apical and basal cells triangular in outline, × 565.

FIG. 11. Embryo showing early differentiation of foot "a," seta "b," and capsule "c," × 565.

The development of the endosperm in Vaccinium corymbosum

Neil E. Stevens

(with four text figures)

The occurrence of a "chambered" embryo sac, formed by the development of a transverse wall following the first division of the primary endosperm nucleus, has been reported in four genera of the Ericaceae. In recent studies of the high bush blueberry, *Vaccinium corymbosum* L., the writer has noted a variation from this of sufficient interest to warrant brief publication.

In 1849 Hofmeister (2) published an account of the development of *Monotropa Hypopitys*. According to his descriptions and figures (*pl. 12, f. 11*) the embryo sac in this species is first cut in two by a cross wall near the middle; afterwards cross walls are formed in each half and the micropylar end is cut off by a wall, thus resulting in an embryo sac of five superimposed cells. Nine years after the publication cited above Hofmeister described the development of *Vaccinium Myrtillus* and *Pyrola rotundifolia* (3), in both of which he found that the development of the endosperm took place as in the *Monotropa* without free nuclear division.

Koch (4), in his studies of *Monotropa Hypopitys*, largely confirms the work of Hofmeister. His figure (*pl. 10, f. 12*) closely resembles that of Hofmeister except that he finds no cross wall near the micropylar end and thus figures a four-chambered, instead of a five-chambered, embryo sac.

In the trailing arbutus, *Epigaea repens*, the writer (5) found a condition much like that reported in other genera. His figure of the *Epigaea* (*f. 3*) very closely resembles Koch's figure of the *Monotropa*, a fact which the writer apparently overlooked in his earlier paper (5, p. 540). The writer also reported the occurrence in the *Epigaea* of haustoria extending out into the tissues of the integument from the ends of the developing endosperm.

The slides of *Vaccinium corymbosum*, on which the present notes are based, were all made from material collected at East

Wareham, Massachusetts, during June, 1916. The material was fixed in a solution of equal parts glacial acetic acid and absolute alcohol, imbedded in paraffin, cut and stained in the usual way. From a study of this material it is apparent that the development of the endosperm of this species may begin in two quite different ways, either by the formation of a cross wall following the first division of the primary endosperm nucleus as has been reported in the other genera of the Ericaceae, or by a period of free nuclear division as has been described in a very large number of species.

FIG. 1 shows a typical two-chambered embryo sac much like those described in *Monotropa* and *Epigaea*. The material examined also showed the four-chambered stage which characteristically follows this. FIG. 2, on the other hand, illustrates an embryo sac which has developed by free nuclear division. The stage represented by FIG. 3 may obviously have resulted from free nuclear division followed by the beginning of wall formation near the center of the embryo sac, or there may have been some free nuclear division after the formation of the cross walls.

FIG. 4 shows a somewhat more advanced stage, in which the irregular arrangement of the cell walls suggests that there was a period of free nuclear division. In this figure the layer of small cells with dense protoplasm (shaded) represents the "tapetum" mentioned in *Epigaea* (5, *f. 4*). The developing haustoria may also be noted. The antipodal haustorium consists of only one cell, while the micropylar haustorium contains three. In the mature seed of *Vaccinium corymbosum* the haustoria are larger than in the seed of *Epigaea repens;* their development also begins relatively early. In *Epigaea* when the embryo is in the eight-celled stage and the endosperm well differentiated both haustoria are still small and consist of but a single cell, whereas in *Vaccinium* the haustoria have attained a considerable size before any divisions of the fertilized egg are apparent.

Hofmeister found that *Vaccinium* (3, p. 141) differed from the other genera described by him in that after the formation of the first wall across the embryo sac, endosperm developed only in the antipodal chamber, while in *Monotropa* and *Pyrola* endosperm developed in both chambers (see also Coulter and Chamberlain, 1, p. 177). The condition found by the writer in *V. corymbosum*

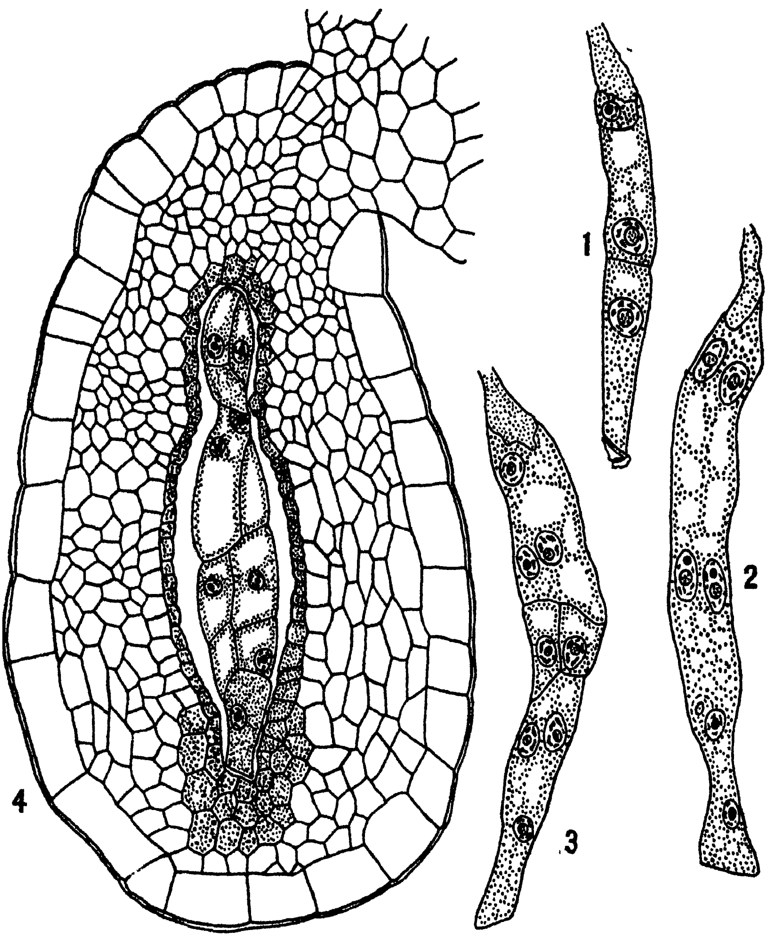

FIG. 1. Longitudinal section of embryo sac of *Vaccinium corymbosum* in two-celled stage; the fertilized egg and the remains of the pollen tube may be seen at the upper end and the remains of the antipodal cells at the lower end. ×290.

FIG. 2. Embryo sac of *V. corymbosum* which shows only free nuclear division. × 290.

FIG. 3. Embryo sac from the same ovary as that in FIG. 2, showing two cross walls and evidence of free nuclear division. × 290.

FIG. 4. Longitudinal section of ovule of *V. corymbosum* showing few-celled endosperm with haustoria developing at either end. The inner cells of the integument are specialized to form a tapetum, being more densely crowded with protoplasm and generally smaller than the other cells of the integument. The walls of the epidermal cells are already somewhat thickened. × 170.

represents a still further variation and suggests the desirability of a careful study of the development of the endosperm in other genera of this family. The writer has, however, been able to examine only one. Slides of *Kalmia latifolia* made from material collected at Vienna, Virginia, on May 28, 1916, showed embryo sacs before division and in the two-celled and four-celled stages. Material collected August 13, 1916, showed the endosperm with haustoria at either end, the whole condition very closely resembling that described in *Epigaea*.

The significance of the condition described in *Vaccinium corymbosum* lies of course in the fact that here occur in a single species types of development hitherto associated with different genera or even different families. All the figures were drawn from material collected from a single plant and FIGS. 2 and 3 represent ovules in the same ovary. Examination of a large amount of material of the other genera described might result in finding variations as marked as those in the *Vaccinium*.

BUREAU OF PLANT INDUSTRY
WASHINGTON, D. C.

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Three South American species of Asterella*

ALEXANDER W. EVANS

The genus *Asterella* has many representatives on the American continent. Most of the northern species are widely distributed, but the southern and tropical species tend to be more restricted in range. Of the fifteen North American species recognized by the writer in his recent revision† only two are known to extend into South America. These are *A. venosa*, which was based on material from Brazil, and *A. lateralis*, which Spruce collected in Ecuador. No other South American stations for either species have been recorded. In the present paper three species which are not known to extend into North America are discussed. Four other South American species have been described by Stephani in his Species Hepaticarum, but no material of these is available at the present time.

1. **Asterella chilensis** (Mont.) comb. nov.

Fimbriaria chilensis Nees & Mont.; Montagne, Ann. Sci. Nat. Bot. II. **9**: 41. 1838.

Hypenantron chilense Trevis. Mem. R. Ist. Lomb. III. **4**: 441. 1877.

Thallus green, becoming brownish or purplish with age, the ventral scales usually more deeply pigmented, mostly 0.5–1 cm. long and 1.5–2.5 mm. wide, in fertile branches broadening out somewhat at the apex, plane or somewhat concave, the thin and slightly wavy margins not incurved when dry, branching normally by forking, sometimes (according to published descriptions) innovating at the apex, keel broad and rounded; epidermis composed of cells with slightly thickened walls, sometimes with more or less evident trigones, averaging about 35 x 25 μ; pores slightly

* Contribution from the Osborn Botanical Laboratory.

† The North American species of *Asterella*. Contr. U. S. Nat. Herb. **20**: 247–312. 1919. In this paper full descriptions may be found of the following species referred to in the present article: *A. elegans* (Spreng.) Trevis., *A. lateralis* M. A. Howe, *A. Lindenbergiana* (Corda) Lindb., *A. Ludwigii* (Schwaegr.) Underw., *A. tenella* (L.) Beauv., and *A. venosa* (Lehm. & Lindenb.) Evans.

elevated, measuring (with their surrounding cells) mostly 90–100 μ in length and 80–90 μ in width, surrounded usually by six (more rarely five or seven to nine) radiating series of cells with two or three cells in each series, radial walls slightly thickened; cells with oil bodies as in *A. tenella;* green tissue loose especially toward the margins, air chambers in two or three layers in the median portion, those of the dorsal layer sparingly subdivided by supplementary partitions and considerably larger than the deeper chambers; compact tissue occupying about two thirds the thickness of the thallus in the median portion, thinning out gradually on the sides and extending about halfway to the margins, composed of thin-walled cells without pits (so far as observed); mycorrhiza present; ventral scales ovate to lunulate, reddish purple throughout or sometimes with bleached appendages, marginal slime-papillae very short-lived, cells containing oil-bodies mostly three to five, scattered, appendages usually borne singly, rarely in pairs, narrowly subulate, scarcely or not at all constricted at the base, mostly 0.3–0.45 mm. long and 0.06–0.12 mm. wide, acuminate, entire (or sometimes, according to Stephani, with a basal spine), the cells mostly 40–60 μ long and 15–35 μ wide: inflorescence paroicous, the antheridia forming a small and vaguely defined group close to the peduncle of the female receptacle: female inflorescence borne on a leading branch, peduncle mostly 1–1.5 cm. high, more or less purple, with small clusters of narrow paleae at base and apex but otherwise naked or nearly so; disc of receptacle green or yellowish, mostly 2–3 mm. across, bluntly conical and usually three- or four-lobed to about the middle, the lobes dilated at the apex, covered over with low coarse tubercles, giving the ends of the lobes a crenate appearance, the involucres broad and undivided, entire or nearly so; pseudoperianths white, extending downward and outward, mostly eight-cleft, the divisions subulate, becoming free with age: capsule wall not studied (hyaline, according to Stephani); spores yellow to brownish yellow, mostly 80–90 μ in diameter, with a thin, wavy, and minutely crenulate wing, 10–16 μ wide along the edges, whole surface covered over with a very fine and irregular reticulum, the meshes mostly 1–5 μ across, formed by a system of delicate anastomosing lines, spherical face showing in addition a coarse reticulum with meshes 16–20 μ across, formed of ridges similar to the wings, plane faces without ridges (so far as observed), margins of wings and ridges more or less broadened; elaters pale yellow, mostly 120–200 μ long and about 6 μ wide, tapering slightly toward the blunt ends, usually with two loosely twisted spirals throughout the entire length.

Known only from Chile; the following specimen has been examined:

CHILE: near Santiago, 1915, *N. Costes* (N. Y.).*

The type material was collected by Bertero near Quillota; Stephani has since reported the species from Pelaquén, *P. Dusén* (in Bih. K. Svensk. Vet.-Akad. Handl. 26 (3^6): 17. 1900).

According to Montagne's account the capsules of the original material were immature, making it impossible to give any data about the spores and elaters. The description of the gametophyte, however, is unusually full and discusses certain histological features which were usually ignored at that time. It calls attention, among other things, to the thallus broadening out from a narrow linear base; to the elevated pores, making the epidermis appear undulate in cross section; to the large air chambers in the green tissue, arranged in a single layer; to the coarsely tuberculate receptacle, three- or, rarely, four-lobed to the middle, with veiny, truncate lobes; to the apical paleae of the peduncle; to the relatively short pseudoperianth, with six to eight divisions, free at maturity. There is little to criticise in his account, except that the undulate appearance of the epidermis is not always striking and that the air chambers are in more than one layer in the median portion of the thallus. As a matter of fact they are in one layer toward the margin, and the more deeply situated median chambers are difficult to demonstrate in dried material. Stephani, in his description, assigns a paroicous inflorescence to the species, noting the androecium at the base of the peduncle, and adds that the spores are yellow, rough, and broadly winged and that the elaters are hyaline and bispiral. He places the species in the same group as *A. tenella*, *A. macropoda*, and *A. Lindenbergiana*, on account of the shape of the receptacle, which he describes as shortly conical and obtuse at the apex

In general appearance *A. chilensis* bears a strong resemblance to *A. tenella* and *A. Ludwigii*, and the species agree further in their dichotomous branching; in their paroicous inflorescence; in their normally eight-cleft pseudoperianths, the divisions of which become free at maturity; and in their yellow spores with broad wings along the edges and a coarse surface-reticulum, at least on the spherical faces. Of course the structure of the green tissue

* In the citation of specimens "N. Y." signifies the herbarium of the New York Botanical Garden and "Y," the herbarium of Yale University.

will at once distinguish the Chilean species, the dorsal air chambers being subdivided by supplementary partitions, while those of *A. tenella* and *A. Ludwigii* remain undivided. The basal portions of the ventral scales, moreover, have fewer cells with oil-bodies and the appendages are much more slender. The deeply lobed female receptacle is also a distinctive feature, the lobes being much shorter in *A. tenella* and scarcely evident in *A. Ludwigii.* In *A. venosa,* with which the species was compared by Montagne, the thallus is far more delicate, the disc of the female receptacle is flatter, the spores are smaller, and there is no coarse reticulum on the surface.

2. **Asterella macropoda** (Spruce) comb. nov.

Fimbriaria macropoda Spruce, Trans. Bot. Soc. Edinburgh **15**: 564. 1885.

Fimbriaria canalensis Spruce, *l.c.* 564. 1885.

Fimbriaria Mandoni Steph. Bull. Herb. Boissier **7**: 207. 1899.

Thallus green above and sometimes throughout but usually with the margin and ventral surface more or less pigmented with purple, mostly 2–3 cm. long and 5–8 mm. wide, plane or nearly so with undulate and often crispate margins, branching by forking and also by apical innovations and intercalary ventral outgrowths, keel narrow but rounded: epidermis composed of cells of somewhat thickened walls, sometimes with distinct trigones, averaging about 28 x 24 μ (exceptional cells sometimes 60 μ long); pores somewhat elevated, measuring (with their surrounding cells) mostly 120–140 μ in length and 100–120 μ in width, surrounded by eight (sometimes seven, nine or, rarely, ten) radiating series of cells with four (sometimes three or five) cells in each series, radial walls distinctly thickened, becoming thinner toward the opening; cells containing oil-bodies as as in *A. tenella;* green tissue loose, the air-chambers in three or four layers (in the median portion), those of the dorsal layer sparingly subdivided by supplementary partitions and thus appearing about as large as the deeper chambers; compact tissue occupying about half the thickness of the thallus in the median portion, thinning out gradually on the sides but extending scarcely more than one-tenth the distance to the margin, composed of cells with slightly thickened, pitted walls: mycorrhiza sometimes present; ventral scales ovate and long-decurrent, purple throughout or with the appendages and margins more or less bleached, cells containing oil-bodies mostly eight to twelve, scattered,

slime-papillae short-lived and inconspicuous, marginal cells smaller and more irregular than the median cells, appendages one or two, usually distinctly constricted at the base, narrowly ovate to lanceolate, mostly 0.35–0.75 mm. long and 0.15–0.35 mm. wide, the apex rarely rounded, usually obtuse, acute or apiculate, the margin entire or vaguely crenulate from projecting cells, cells averaging about 45 x 25 μ, one or two smaller cells with oil-bodies often present: inflorescence autoicous: male inflorescence borne on a very short ventral branch (so far as observed), consisting of a cluster of antheridia, variable in number, and destitute of marginal paleae, ostioles short: female inflorescence variable in position, sometimes borne on a branch of a dichotomy, sometimes on a ventral branch, variable in length; peduncle mostly 1.5–5 cm. long, with very long scattered paleae and an apical cluster, more or less pigmented with purple; disc of receptacle often purple, mostly 4–7 mm. across, delicate in texture, the center depressed-hemispherical, mostly four-lobed to about the middle, the lobes spreading almost horizontally, broadening out and separated by sharp sinuses, upper surface covered over with coarse tubercles, making the margins appear crenate, involucres green to purple, undivided, entire or nearly so, not reaching the margins of the lobes; pseudoperianth extending downward and outward, yellowish brown at the base and rarely throughout, usually for the most part deep vinous purple, mostly twelve- to sixteen-cleft, the divisions becoming filiform upon drying, coherent at the apex: capsule brown to purple, circumscissile by an irregular line; spores brown, translucent, mostly 80–90 μ in diameter, with thin and wavy, minutely crenulate wings 12–14 μ wide along the edges, entire surface minutely and closely punctulate or with short and irregular lines, spherical face showing in addition a coarse and usually regular reticulum, the meshes mostly 20–30 μ across, enclosed by the marginal wings and a series of similar anastomosing ridges, each plane face with a similar but often incomplete reticulum, margins of wings and ridges darker and somewhat thicker, marked by subparallel lines, and often showing minute interstices especially at points of junction; elaters brown, variously curved, mostly 300–360 μ long and 8–10 μ wide, tapering slightly to the blunt ends, mostly bispiral throughout.

On rocks and banks of streams; known only from the Andes. The following specimens have been examined:

ECUADOR: Quito, *W. Jameson* (N. Y., listed by Mitten, as *Fimbriaria elegans*, in Jour. Bot. & Kew Misc. 3: 361. 1851); Pichincha, *R. Spruce* (N. Y.; type of *Fimbriaria macropoda*,

distributed in Hep. Spruceanae); Canelos, *R. Spruce* (N. Y., Y.; type of *F. canelensis*, distributed in Hep. Spruceanae).

Stephani lists *Fimbriaria Mandoni* from the following locality: BOLIVIA: Sorata, *G. Mandon*.

In proposing *Fimbriaria macropoda* as a new species Spruce cited no specimens except those which he himself had collected "in rivuli ripis montis Pichincha." In Stephani's monograph the species is still restricted to the "Andes quitenses," but Jameson, Lindig and Wallis are mentioned as collectors, in addition to Spruce. Stephani states, in fact, that he had not seen Spruce's original material at all. Unfortunately he gives no further information about the specimens which he cites, but it is possible to draw certain inferences from the fact that he does not allude to Jameson, Lindig or Wallis elsewhere in connection with the genus. There is a probability, for example, that Jameson's specimens are those from Quito, listed by Mitten under the name *F. elegans*. There is a further probability that Lindig's specimens are those which Gottsche* referred to *F. Lindenbergiana* on account of their violet-colored capsules. They were collected at Boqueron and Tocarema, in the province of Bogotá, Colombia; and, although these stations are not actually in the "Andes quitenses," they are assuredly in the same general mountainous district. There is also a possibility that Wallis's specimens may have come from Colombia, where most of his South American Hepaticae were collected. Unfortunately the writer has been unable to consult the specimens in question, so that it is impossible to support these inferences by direct evidence.

In Spruce's original description many of the distinctive features of the species are clearly brought out. The delicacy and translucency of the thallus, for example, are emphasized and attention is called to the purple pigmentation of the margin and ventral surface; to the small number of epidermal pores present; to the narrow midrib; to the very long peduncle of the female receptacle, with scattered paleae and a denser cluster at the apex; to the deeply four-lobed disc, covered over with tubercles; to the membranous involucre, narrower than the lobes; to the rose-purple segments of the pseudoperianth, connate at the apex; and

* Ann. Sci. Nat. Bot. V. 1: 187. 1864.

to the large spores with the outer wall pellucid and "laxe celluloso" (in apparent allusion to the coarse surface-network). Spruce ascribed a dioicous inflorescence to the species, probably because the male branches escaped his notice, and stated further that ventral branches were lacking, that apical dichotomies were very rare, that the female inflorescence was terminal (presumably on the main thallus or on one of its innovations), and that the pseudoperianth was definitely twelve-cleft.

Stephani, in his description, states that the sexual branches are ventral in position and at least implies that forking is less uncommon than Spruce indicates. He definitely assigns an autoicous inflorescence to the species and emphasizes the minuteness of the male branches. He also describes certain structural features omitted by Spruce, such as the green tissue with narrow air chambers and the elevated epidermal pores, each surrounded by six radiating series of cells with four cells in a series. In this last characterization no allowance is made for variability, and the same criticism would apply to his account of the appendages of the ventral scales. According to his statements these are borne in pairs and are approximate, elongated, parallel, lanceolate, and composed of very irregular cells. In the writer's experience the appendages are often borne singly—the only condition mentioned by Spruce—and, although the parallel position of paired scales is sometimes striking, it is by no means constant. Stephani's description of the spores as 63 μ in diameter, yellowish, and broadly "lobate cristate" might also be amplified to advantage.

Spruce's *F. canalensis* was based on material which grew on wet and shaded rocks. As emphasized in the original description the plants are extremely delicate, and the thallus shows almost no signs of pigmentation except on the appendages of the ventral scales. Stephani throws doubt upon the constancy of these features, suggesting that plants of less sheltered situations might perhaps be more robust, and the writer feels that these doubts are amply justified. It may be further shown that the points of resemblance brought out in the descriptions of *F. canalensis* and *F. macropoda* are many and important, while the differences are either insignificant or inconstant, this being true not only of those drawn from the texture and color but also of those drawn from

other structural features. The writer therefore feels compelled to regard the two species as synonyms and maintains the specific name *macropoda* because *F. macropoda* precedes *F. canalensis* in Spruce's work. A careful study of the specimens listed above (which include the types of both species) has also shown that this reduction to synonymy is warranted.

Among the resemblances mentioned by Spruce the following may be cited as important: the narrow midrib; the terminal female receptacle; the slender paleae of the peduncle, clustered at the apex but scattered elsewhere; the tuberculate disc, four-lobed to the middle; and the violet-colored divisions of the pseudoperianth. Stephani adds that the inflorescence in both is autoicous, that the minute male inflorescences are borne on short ventral branches, and that the elaters are bispiral. Among the differences brought out by Spruce it will be sufficient to note the following: in *A. canalensis* the thallus is elongated, the appendages of the ventral scales are lanceolate-subulate, the peduncle is short and the pseudoperianth is sixteen- (or seventeen-) cleft; while in *A. macropoda* the thallus is ovate-oblong, the appendages of the ventral scales are obliquely triangular and acuminate, the peduncle is long, and the pseudoperianth is twelve-cleft. Stephani describes or implies certain further differences in the epidermal pores, in the ventral scales, in the discs of the female receptacles, and in the spores; but a careful scrutiny of his statements, as well as those quoted from Spruce will at once make it evident that these differences would easily come within the range of variability to be expected in the organs concerned.

The writer regrets that no specimens of *F. Mandoni* have been available for study and that the reduction of this species to synonymy might therefore be considered unjustifiable. A careful comparison of Stephani's descriptions, however, will show that the characters separating it from *F. macropoda* are exceedingly questionable, and that most of the organs are described in essentially equivalent phrases. Perhaps the most important differences indicated are those drawn from the ventral scales and the spores. In *F. Mandoni* the appendages of the scales are said to be lanceolate, strongly attenuate, and filiform at the apex, and the spores are described as 90 μ in diameter and broadly lobate-

winged; in *F. macropoda* (as already noted) the appendages are said to be merely lanceolate (nothing further being stated about the apices), and the spores are described as 63 μ in diameter and lobate-cristate. It has aleady been shown that the spores of *F. macropoda* usually (if not always) exceed 63 μ in diameter; and it will at once be obvious that the other differences noted are of very slight significance.

A. macropoda occupies a somewhat unique position in the genus. The structure of the green tissue and the frequent occurrence of a female inflorescence on a long branch derived from a dichotomy indicates a relationship with *A. Lindenbergiana* and *A. venosa*, while the short ventral male branches and the not unusual occurrence of a female inflorescence on a more or less abbreviated ventral branch indicates a relationship with *A. elegans*. Perhaps the relationship to *A. Lindenbergiana* is as close as any, the deep purple pseudoperianths being a very striking feature which both species exhibit. The spores, however, are essentially unlike, those of *A. macropoda* being brown and covered over with a coarse network, while those of *A. Lindenbergiana* are purple and covered over with a much finer and more irregular network. *A. Lindenbergiana* is further distinguished by its more extensive compact tissue and sharper keel, by its smaller and usually narrower scale-appendages, by its frequently paroicous inflorescence, and by the shorter lobes of its female receptacle. From *A. venosa*, with which Spruce compares his species, it differs in the possession of lateral intercalary branches, in its larger epidermal pores and less extensive compact tissue, in its autoicous inflorescence, in its purple pseudoperianths with more divisions, and in its darker, larger and coarsely reticulate spores.

3. **Asterella boliviana** (Steph.) comb. nov.

Fimbriaria boliviana Steph. Spec. Hepat. **6**: 11. 1917.

Thallus yellowish green above, usually purple on the ventral surface and along the margin, mostly 1–1.5 cm. long and 4–6 mm. wide, more or less concave, especially when dry, the margins vaguely undulate-crispate, sometimes erect or incurved when dry, branching intercalary and lateral (so far as observed), keel broad and rounded: epidermis composed of cells with distinctly thickened walls, sometimes with indefinite trigones, averaging about 48 x

24 μ; pores elevated, measuring (with their surrounding cells) mostly 100–120 μ long and 70–100 μ wide, surrounded by seven or eight (rarely six or nine) radiating series of cells with three (rarely four or two) cells in each series, radial walls more or less thickened; cells containing oil bodies as in *A. elegans;* green tissue compact, the air chambers narrow, in three or four layers in the median portion of the thallus, those of the dorsal layer abundantly subdivided by vertical supplementary partitions not reaching the epidermis in the vicinity of the pores; compact tissue occupying little more than half the thickness of the thallus in the median portion, thinning out rather abruptly in the sides and extending about halfway to the margin, composed of cells with slightly thickened, pitted walls; mycorrhiza not observed; ventral scales ovate to lunulate, pigmented throughout with a reddish purple or with more or less bleached appendages, cells containing oil-bodies numerous, mostly thirty to sixty, usually scattered but sometimes in pairs or small clusters, tending to be more numerous toward the margin, marginal slime papillae short-lived and inconspicuous, appendages borne singly or in pairs, lanceolate to narrowly ovate merging gradually into the basal portion and scarcely or not at all constricted at the base, mostly 0.7–1.3 mm. long and 0.3–0.35 mm. wide, margin entire or vaguely crenulate or denticulate from projecting cells, acuminate or abruptly apiculate or cuspidate, often tipped with a filament variable in length and variously curved, hooked or contorted, the cells very irregular usually including several with oil-bodies, averaging in the median portion about 70 x 30 μ: inflorescence autoicous: male inflorescence borne on a short and slightly expanded ventral branch, the antheridia forming an irregular median cluster without marginal paleae (so far as observed), ostioles low; female inflorescence borne on a slightly longer and more expanded ventral branch; peduncle more or less pigmented with purple, 1–2 cm. long when well developed, bearing a loose cluster of filiform paleae at the apex and scattered paleae elsewhere; disc of receptacle about 4 mm. wide, bluntly conical, more or less purple, shortly four-lobed, the lobes extending obliquely outward, surface bearing very low and coarse tubercles, especially on the lobes, giving the latter a crenate appearance, involucre not examined; pseudoperianth more or less splotched with purple, mostly eight- to ten-cleft, the divisions subulate, loosely connate at the apex and apparently becoming free at maturity: capsule wall not examined; spores brown or yellowish brown, mostly 90–110 μ in diameter, with wavy, minutely crenulate wings 12–14 μ wide along the edges, spherical face covered over with a coarse and fairly regular network, the meshes mostly 16–20 μ across, formed by a series of anastomosing ridges

similar to the marginal wings, plane faces with similar but more irregular networks, surface otherwise irregularly punctate and marked with fine and irregular lines, especially along the broadened out and darker margins of the wings and ridges, sometimes tending to form secondary and finer networks within the meshes of the coarse network; elaters brown or reddish brown, somewhat curved or often nearly straight, mostly 180–240 μ long and 12–16 μ wide, tapering toward the rounded ends, usually with two or three spirals in the median portion and one or two at the ends.

Known only from Bolivia; the following specimens have been examined:

BOLIVIA: without definite localities or dates, *M. Bang* (N. Y.; two specimens, one numbered *1869*, the other not numbered).

The type locality is described by Stephani as follows: "Hab. Bolivia. (Bong. legit)." In all probability "Bong." is a misprint for "Bang," and the specimens listed above represent a portion of the original material, but this cannot be proved at the present time.

The original description of this distinct and interesting species is far from complete and makes no mention whatever of the epidermis, the green tissue, the spores or the elaters. The author emphasizes the robust and rigid thallus, the ventral and short sexual branches, and the large disc (6 mm. in diameter, according to his statements), semiglobose at the vertex and slightly constricted. He notes further the presence of four campanulate involucres, with large truncate mouths, without saying anything about the lobes of the receptacle, and he describes the ventral scales as large and purple, bearing a large, broadly oval appendage with a long hooked bristle at the apex. The material examined by the writer shows that the ventral scales are more variable than this description indicates and that the hooked apical bristle, although sometimes distinct, is usually represented by a straight or variously contorted or curved bristle. It shows, moreover, the frequent presence of two appendages. Unfortunately the specimens are insufficient to establish an autoicous inflorescence beyond a doubt, only one male branch having been observed; the features of the involucre have likewise been left undetermined in order to avoid the sacrifice of one of the few receptacles, but there is no reason for supposing that the involucre is in any way distinctive.

In the structure of the thallus, in the restriction of the sexual organs to ventral branches, and in many of the characters derived from the female receptacles and the spores, *A. boliviana* shows a close relationship to *A. elegans* and especially to *A. lateralis*. It differs from both of these species in the broader and usually longer appendages of the ventral scales, which are usually much more abruptly contracted into an apical cilium and which are further distinguished by shorter cells and by the frequent occurrence of cells with oil-bodies. In the basal portions of the scales the cells with oil-bodies are unusually abundant, numbering at least twice as many as in *A. elegans* and often five to ten times as many. The elaters of *A. boliviana*, moreover, usually show two spirals at the ends, while those of *A. elegans* and *A. lateralis* usually show only one.

In distinguishing *A. boliviana* from *A. elegans* further characters of importance may be drawn from the sexual branches, the androecia, and the female receptacles. In *A. boliviana* the sexual branches (so far as known) are invariably short; the antheridia form a vaguely defined group without marginal paleae; and the female receptacle is covered over with very short tubercles, scarcely apparent in the central portion: in *A. elegans* the sexual branches vary greatly in length; the antheridia are in a clearly defined and elevated group, surrounded by marginal paleae; and the female receptacle is hemispherical in the center and covered over with longer and more conspicuous tubercles. Some of the characters which separate *A. boliviana* from *A. elegans* are shared by *A. lateralis*, but aside from the important differences derived from the ventral scales and elaters certain other differences derived from the spore markings deserve mention. In *A. lateralis*, except for the coarse reticulum, the spore surface is covered over with crowded and minute dots but not with lines; in *A. boliviana* the surface shows both dots and lines, the latter sometimes anastomosing and thus forming secondary reticula within the meshes of the coarse reticulum.

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INDEX TO AMERICAN BOTANICAL LITERATURE

1914-1919

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense

Reviews, and papers that relate exclusively to forestry, agriculture, horticulture, manufactured products of vegetable origin, or laboratory methods are not included, and no attempt is made to index the literature of bacteriology. An occasional exception is made in favor of some paper appearing in an American periodical which is devoted wholly to botany. Reprints are not mentioned unless they differ from the original in some important particular. If users of the Index will call the attention of the editor to errors or omissions, their kindness will be appreciated.

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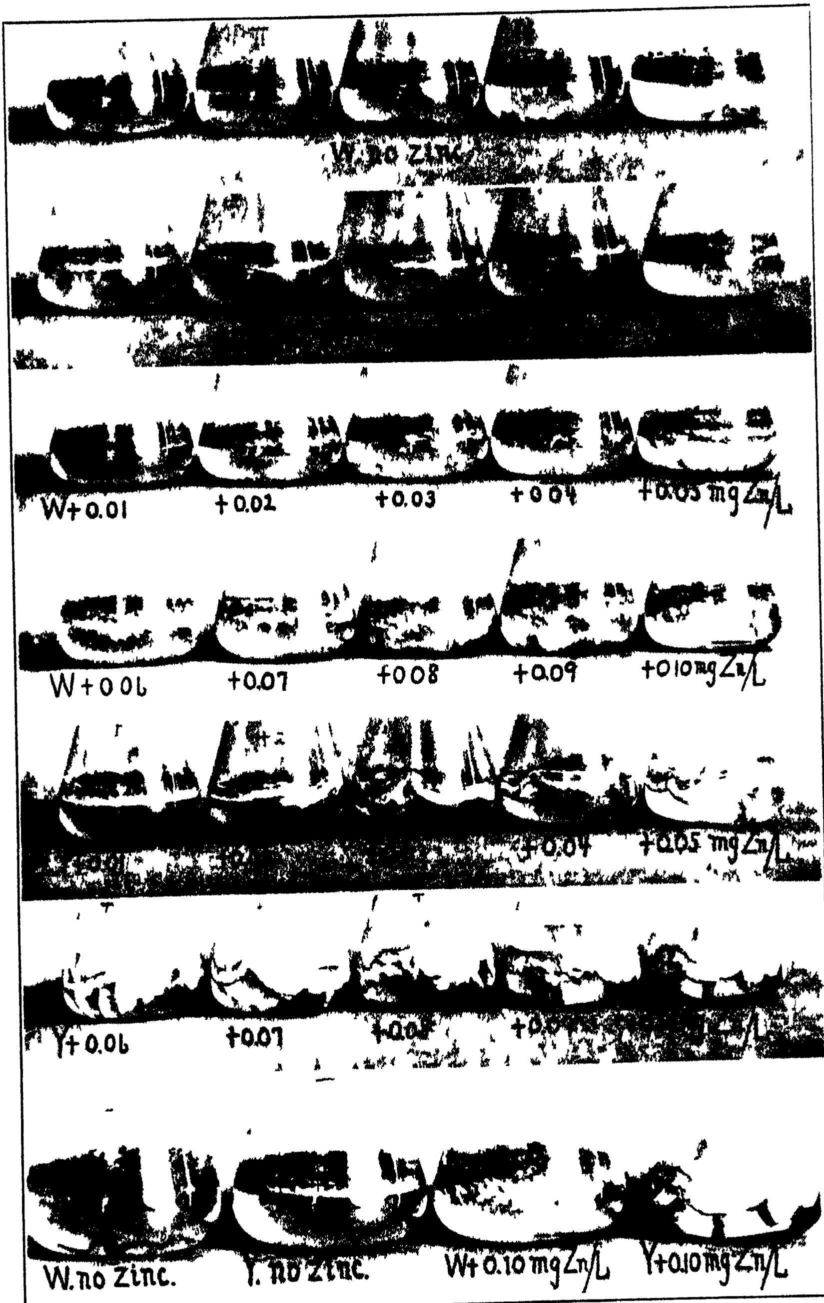
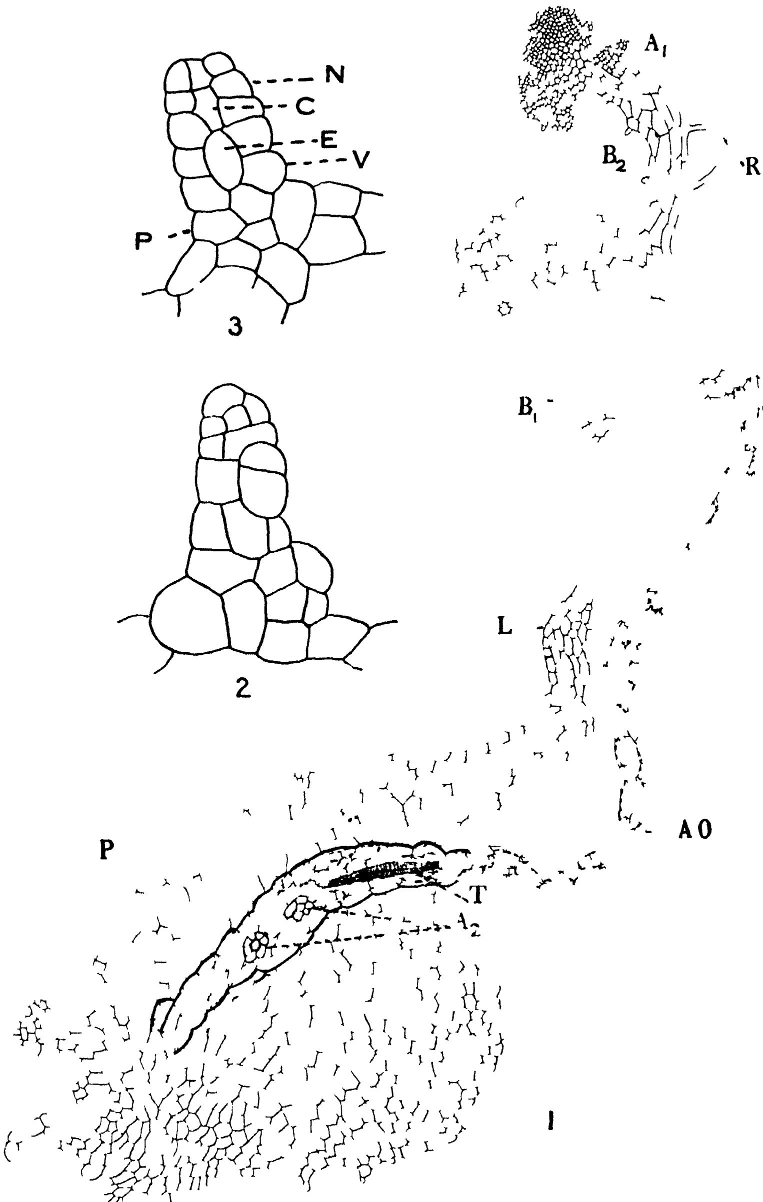
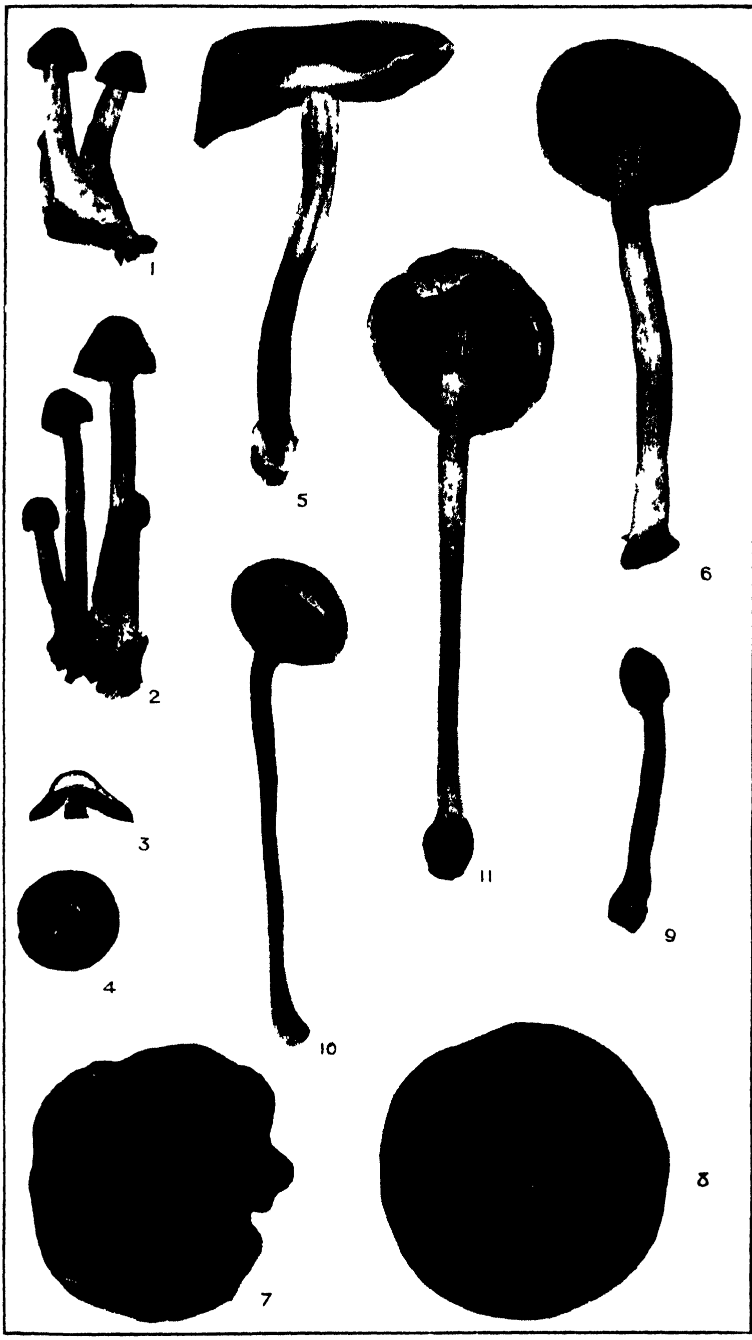
New names and the final numbers of new combinations are in **bold face type.**



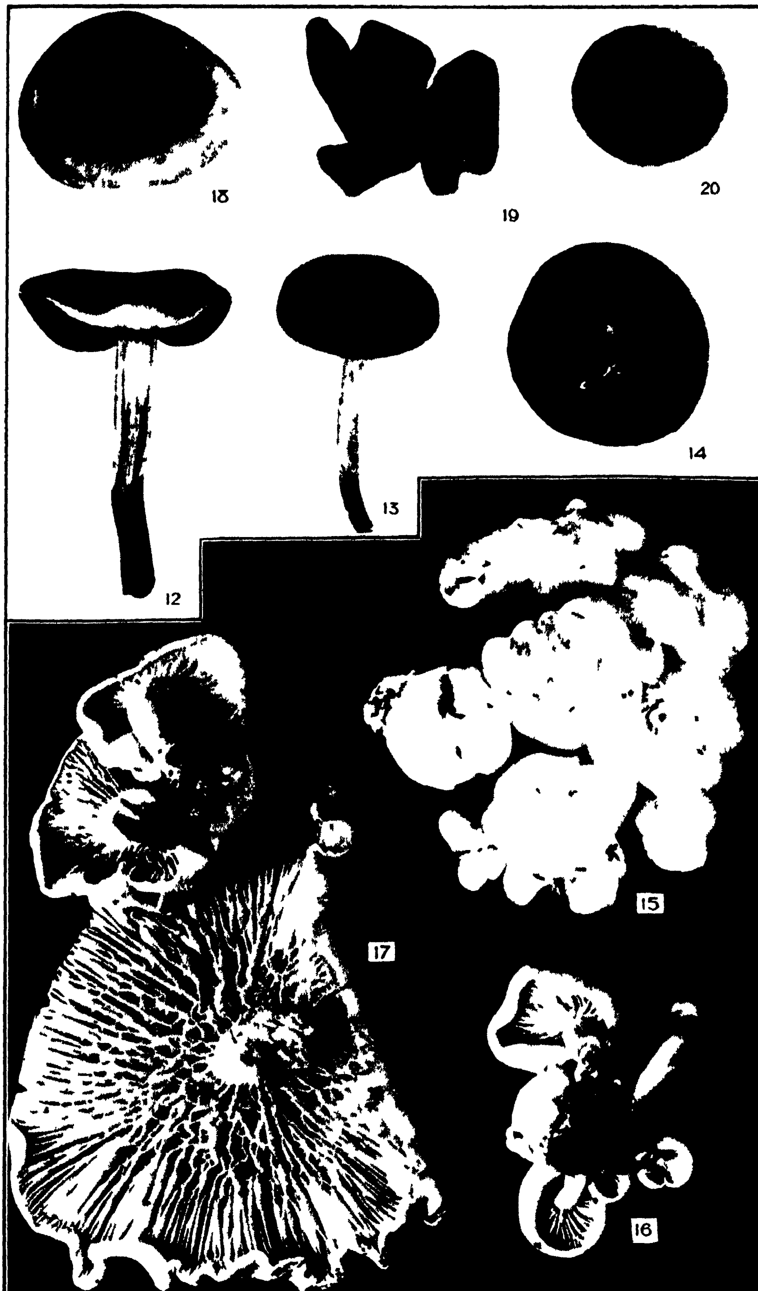
STEINBERG: GROWTH OF ASPERGILLUS NIGER



BROWN: APOGAMY IN CAMPTOSORUS RHIZOPHYLLUS



LEVINE: NON-EDIBLE MUSHROOMS



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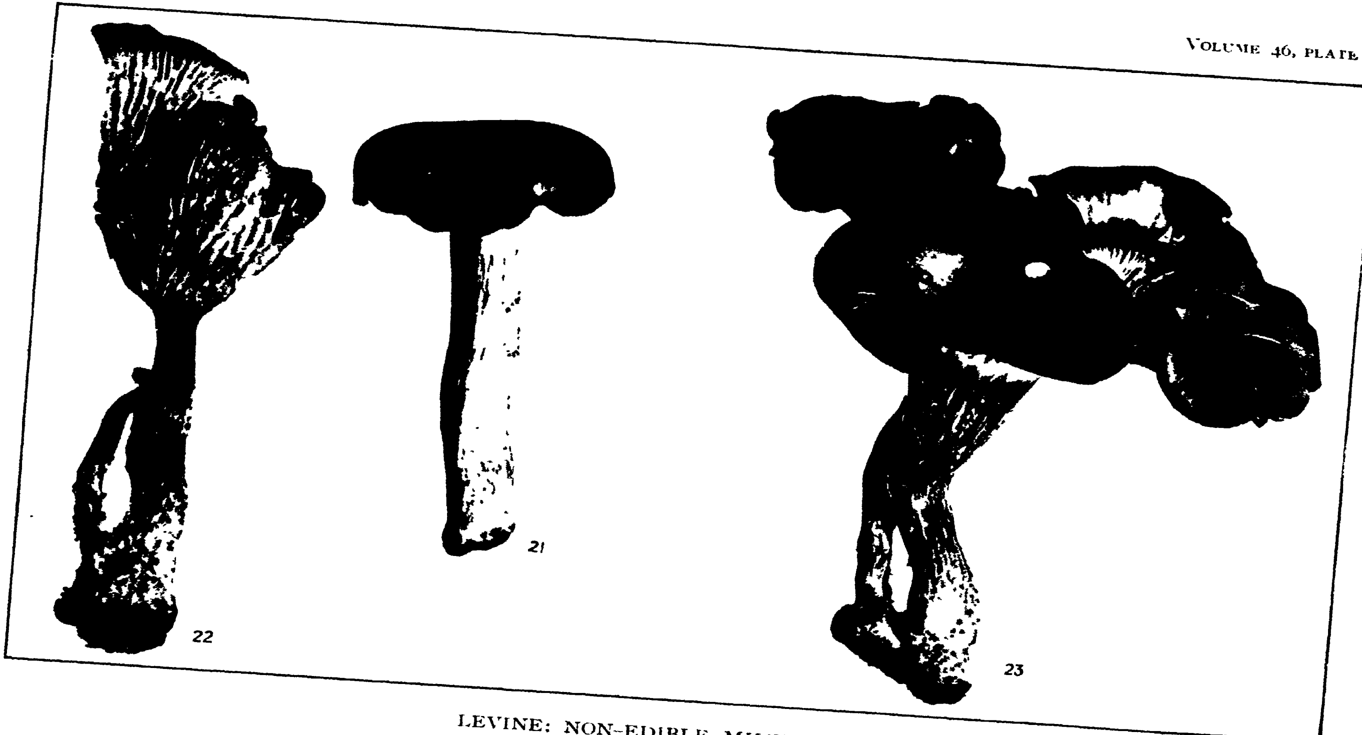

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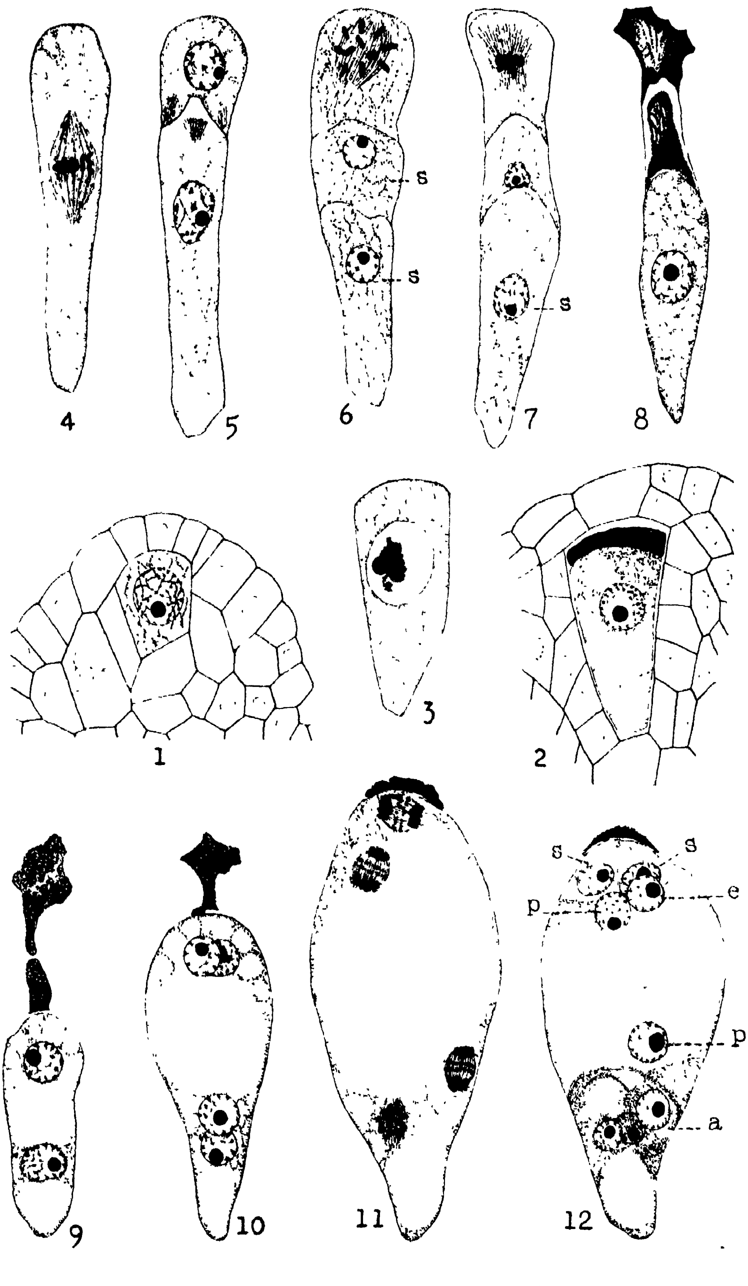
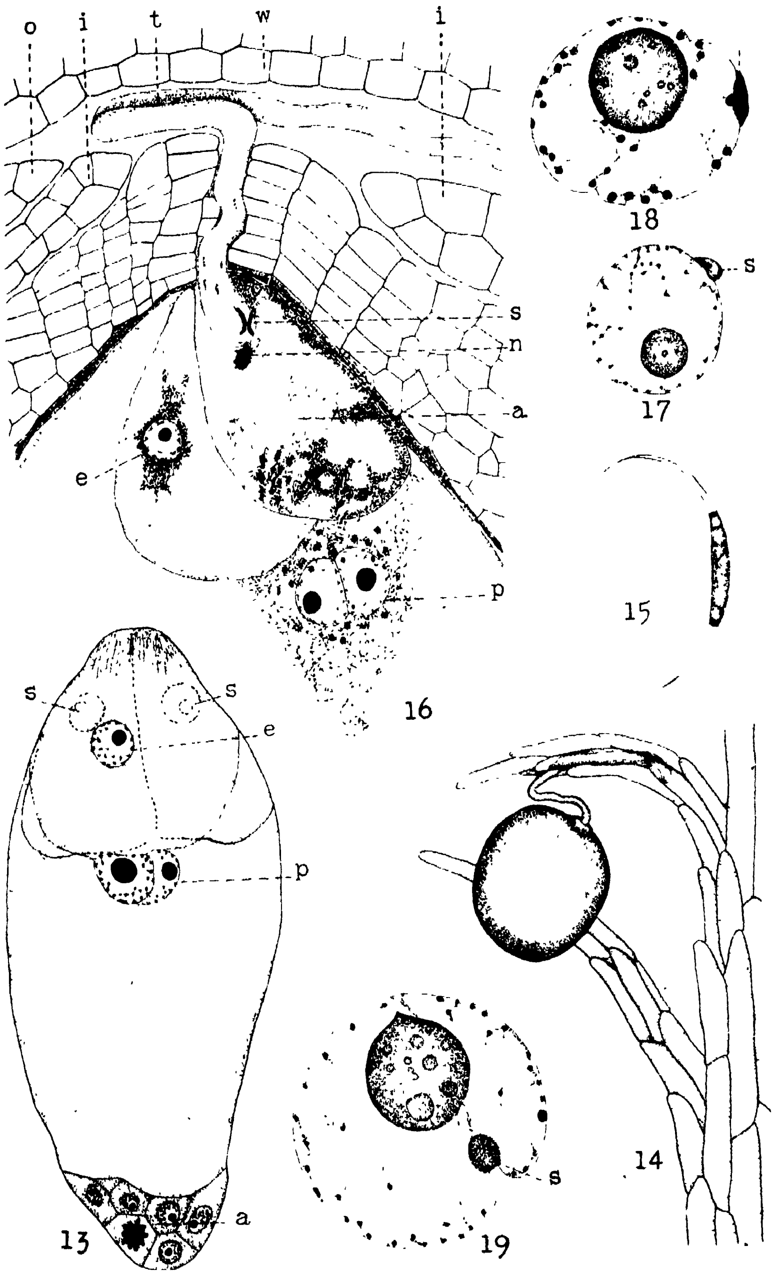
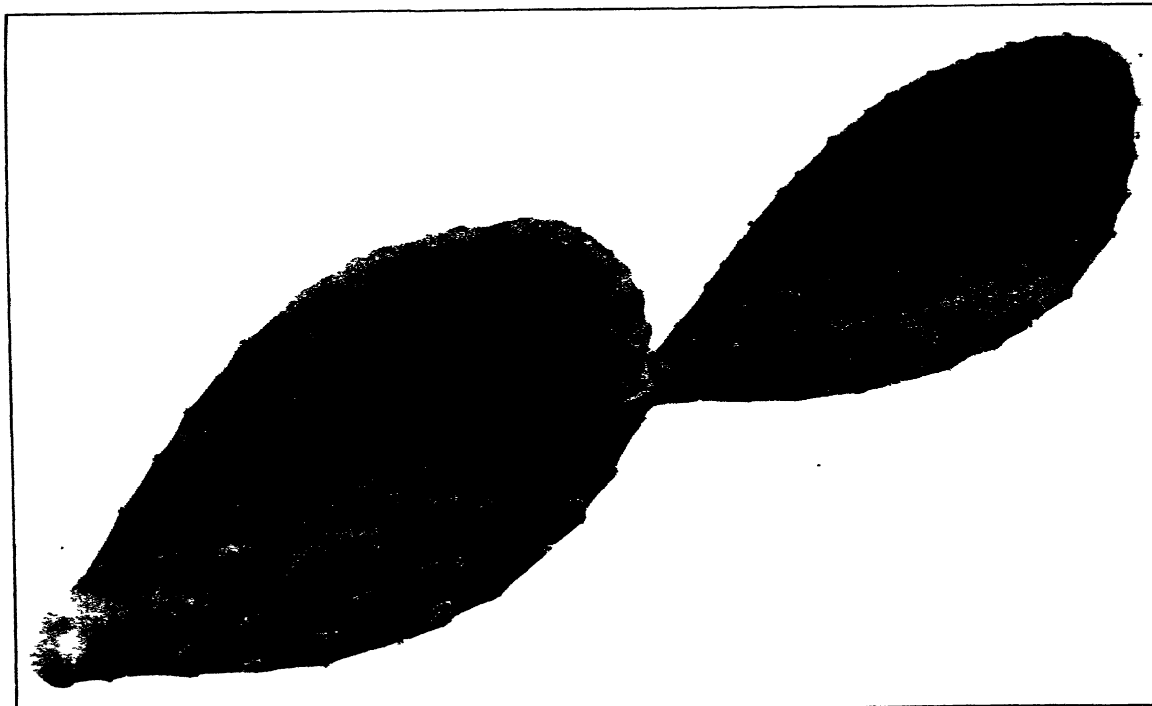


WEATHERWAX: GAMETOGENESIS AND FECUNDATION IN ZEA MAYS



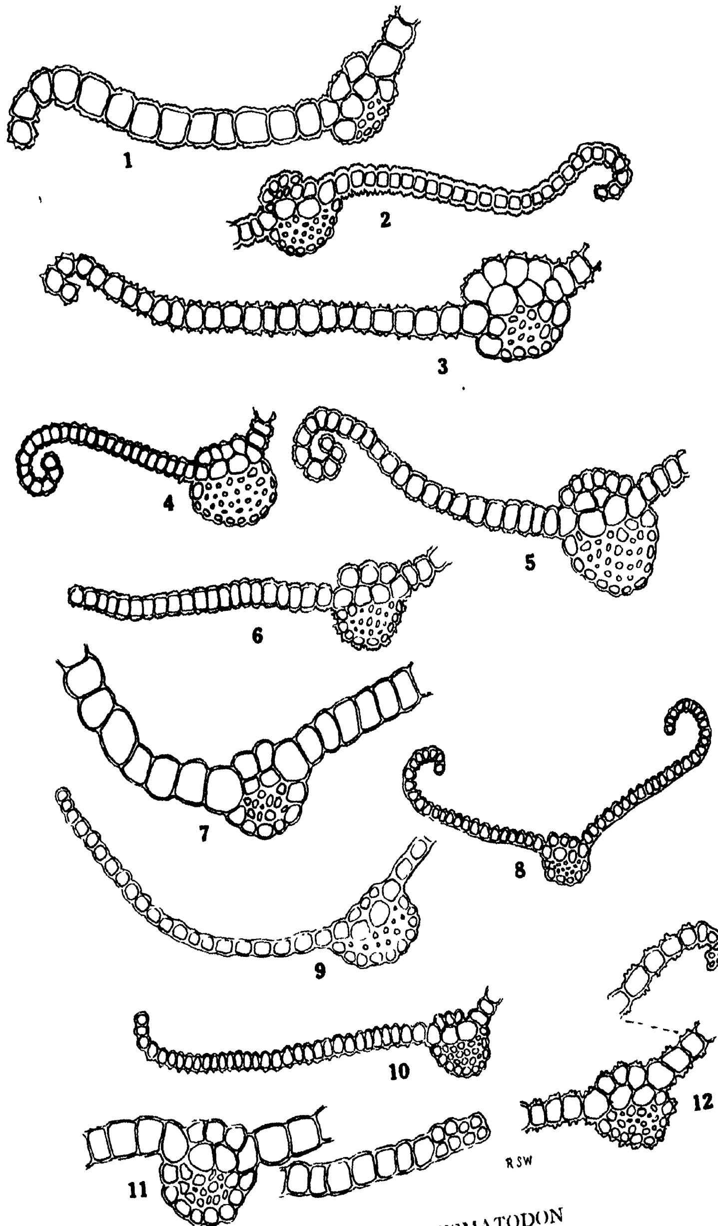
WEATHERWAX: GAMETOGENESIS AND FECUNDATION IN ZEA MAYS

STEWART: MUCILAGE OR SLIME FORMATION IN THE CACTI



OPUNTIA DIVERSISPINA Griffiths

OPUNTIA MARITIMA Raf.



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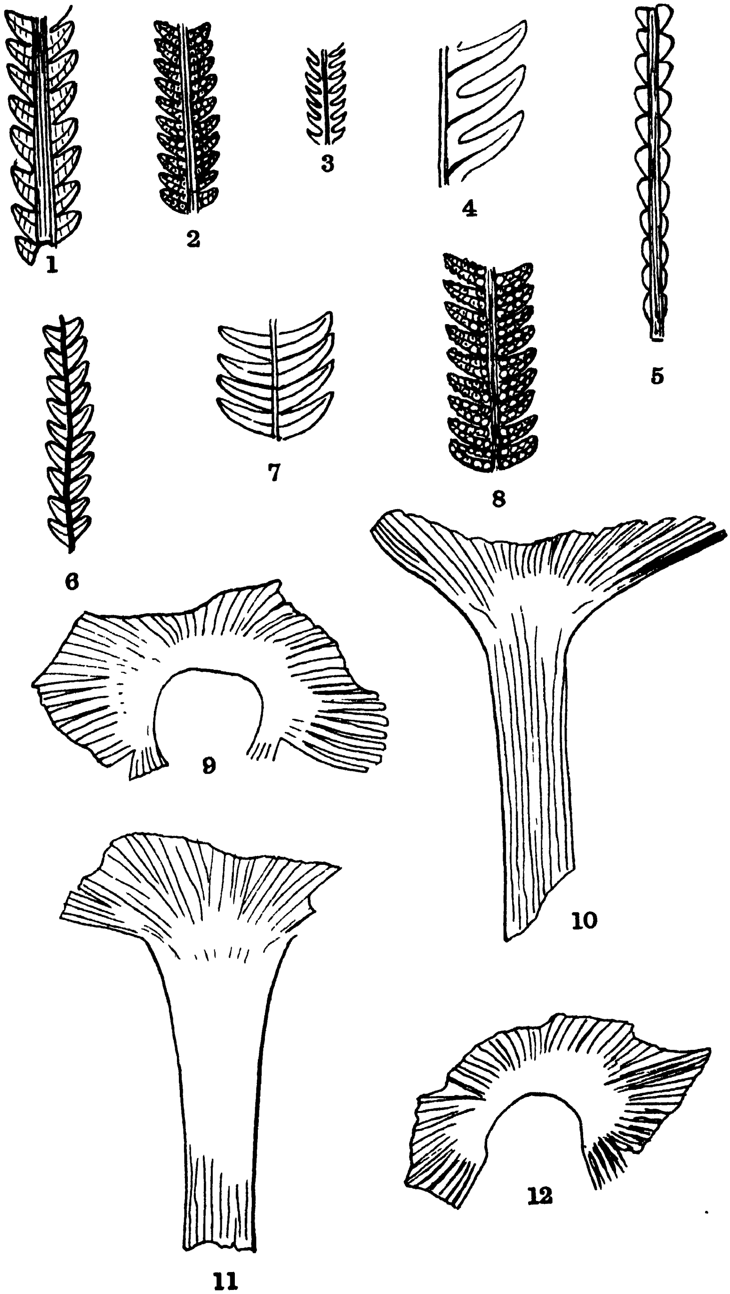
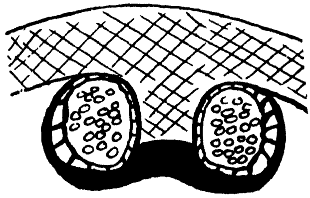


MATONIDIUM AMERICANUM BERRY



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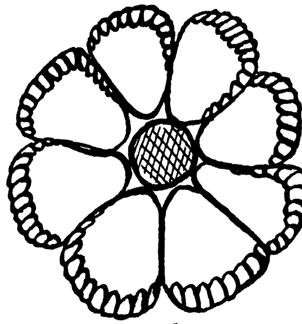

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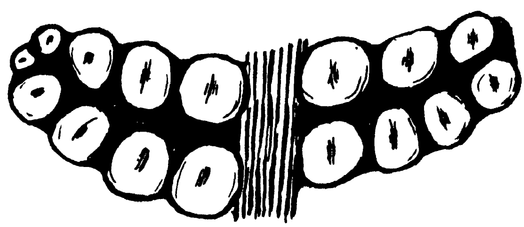

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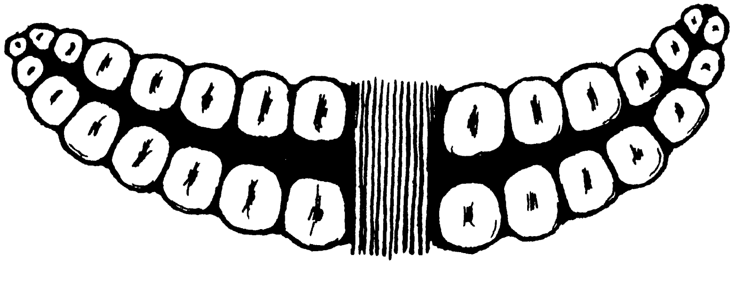
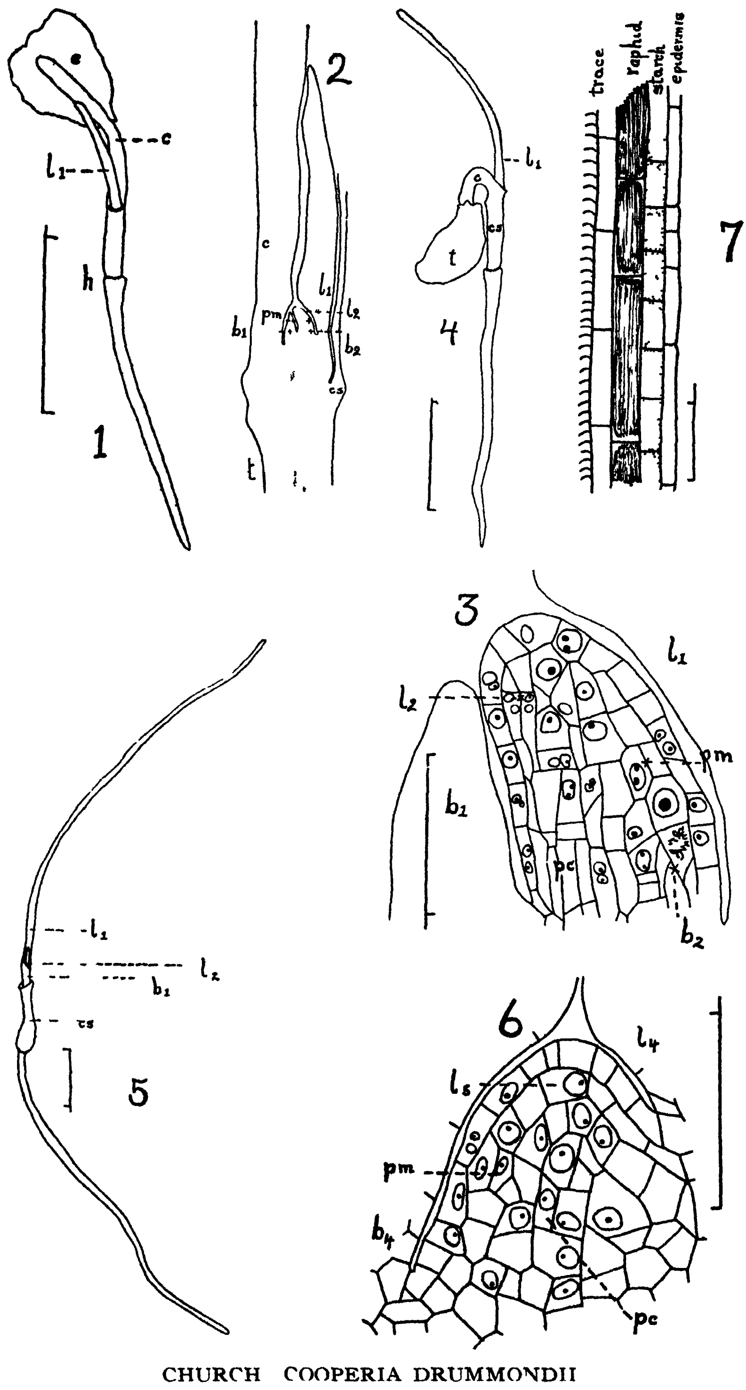
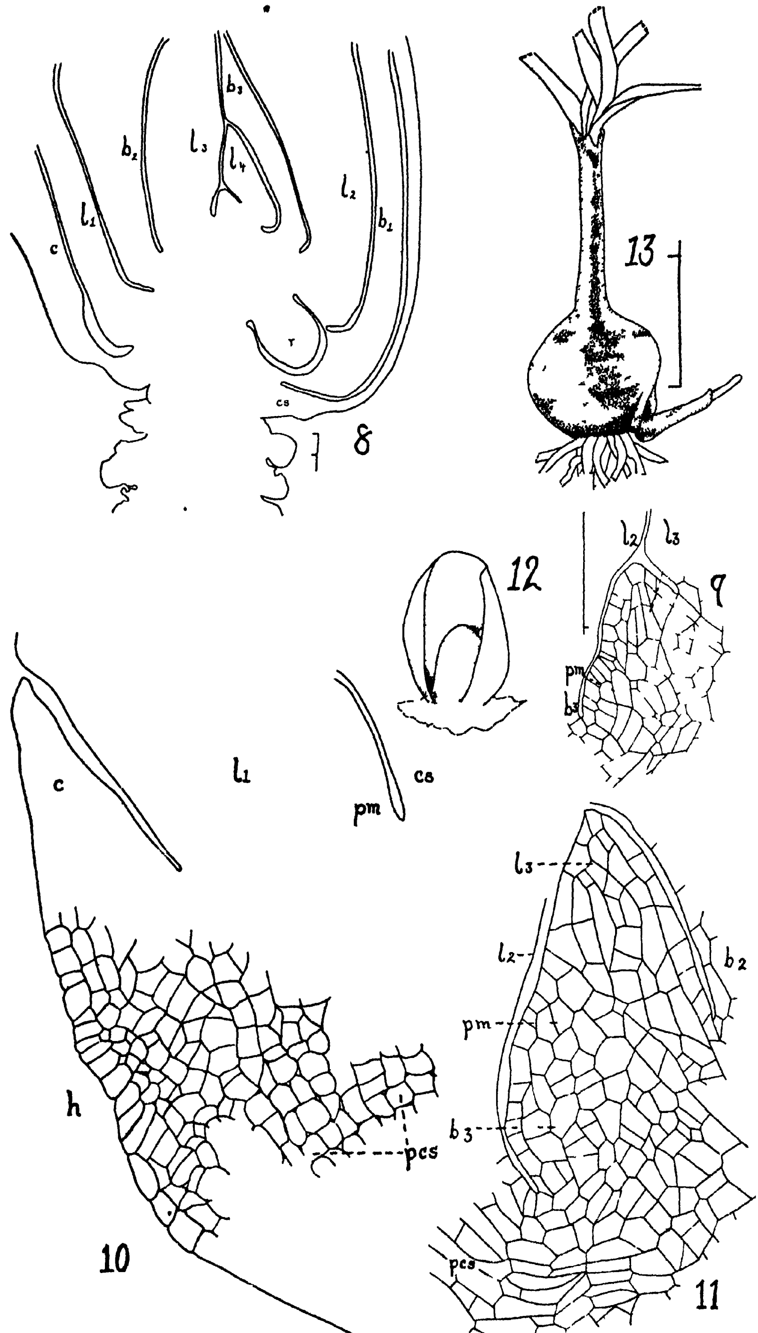


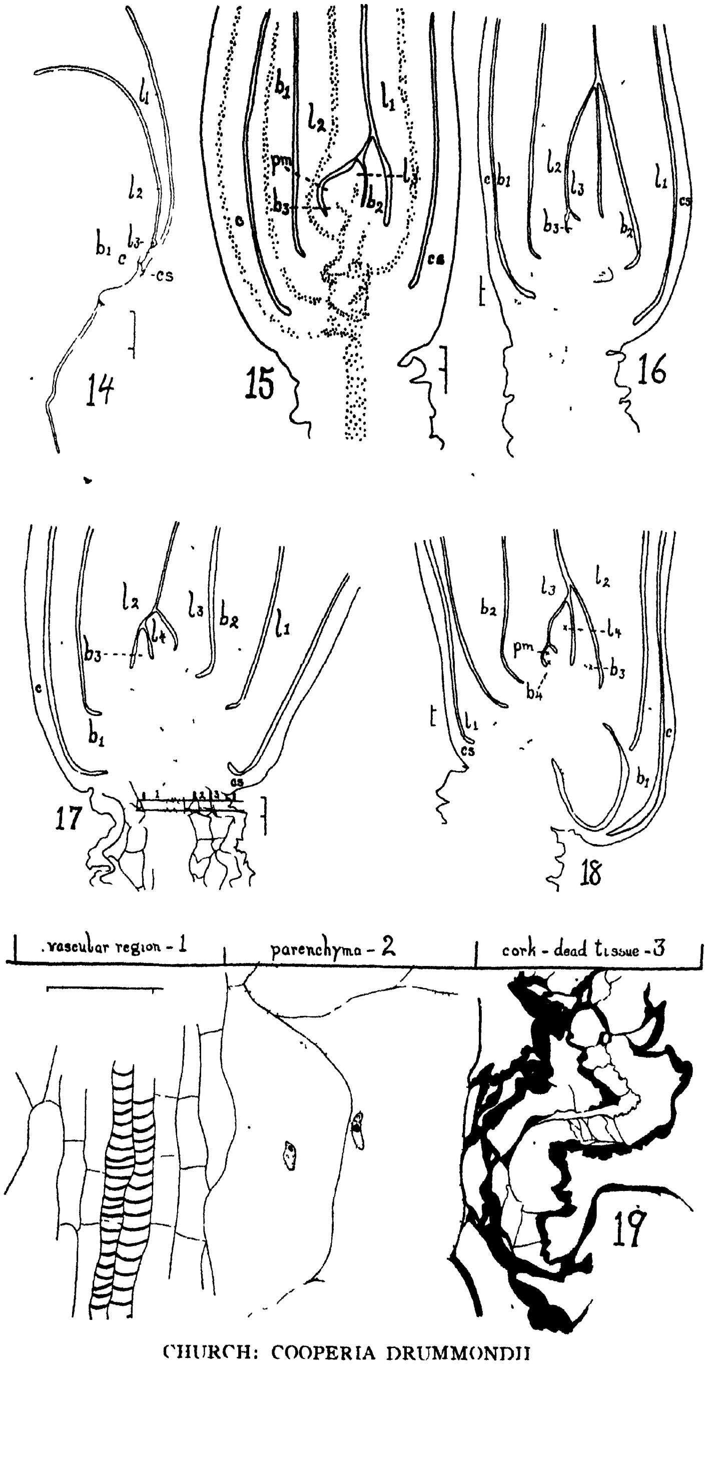
1, 2. MATONIA PECTINATA R.BR.
3–6. MATONIDIUM AMERICANUM BERRY



CHURCH COOPERIA DRUMMONDII



CHURCH COOPERIA DRUMMONDII



CHURCH: COOPERIA DRUMMONDII

LEVINE: PLANT CANCERS

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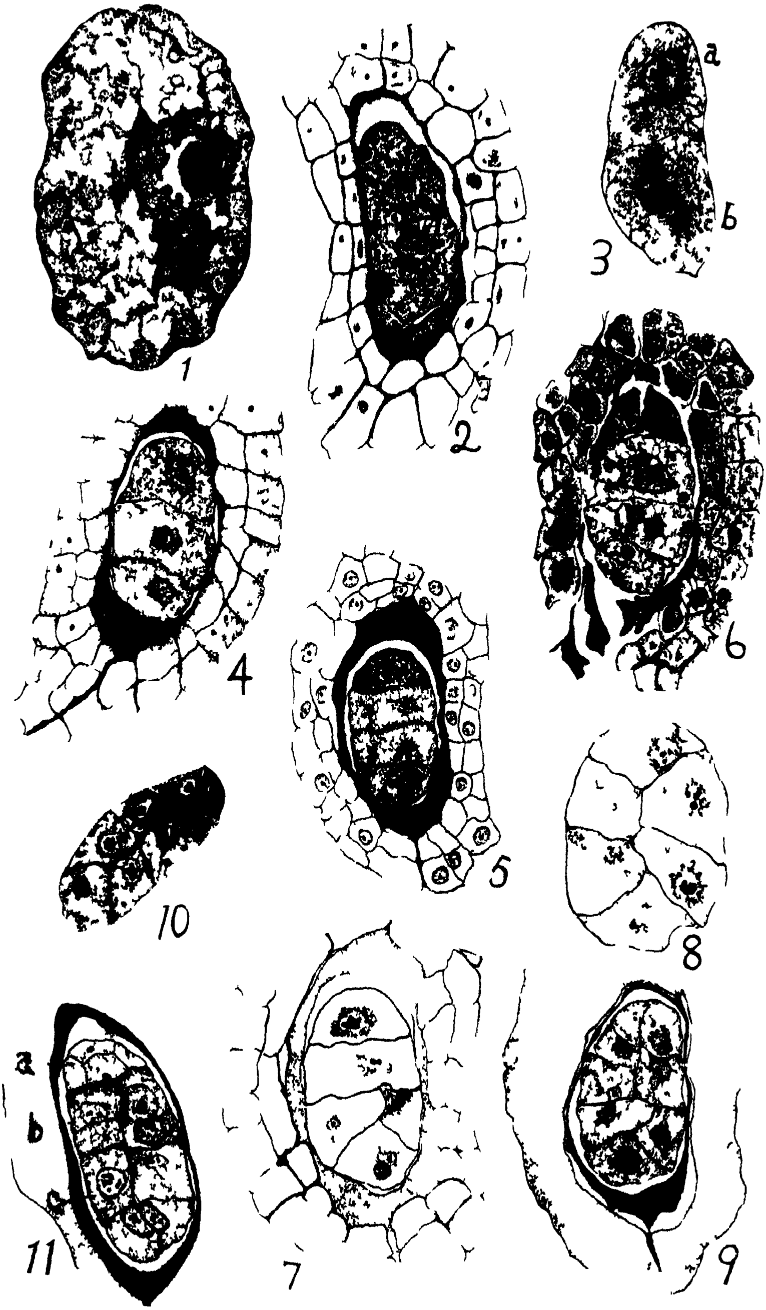
LEVINE: PLANT CANCERS



WOODBURN: EMBRYOLOGY OF REBOULIA